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2.2. MAMMALS

Table 2-2 lists the mammalian species described in this section. For range maps, refer to the general references identified in the individual species profiles. The remainder of this section is organized by species in the order presented in Table 2-2. The availability of information in the published literature varies substantially among species, as is reflected in the profiles. Some of the selected species include two or more subspecies; these are indicated in the profiles when reported by the investigators. Body lengths of the mammals are reported for the length of the outstretched animal from the tip of the nose to the base of the tail. The tail measurements do not include the hairs at the tip, but only the tail vertebrae. Body weight is reported as fresh wet weight with pelage, unless otherwise noted.

Table 2-2. Mammals Included in the Handbook

Order Subfamily	Common name	Scientific name	Section
Soricidae	short-tailed shrew	Blarina brevicauda	2.2.1
Canidae	red fox Vulpe	es vulpes 2.2.2	
Procyonidae	raccoon	Procyon lotor	2.2.3
Mustelidae Mustelinae Lutrinae	mink river otter	Mustela vison Lutra canadensis	2.2.4 2.2.5
Phocidae	harbor seal	Phoca vitulina	2.2.6
Cricetidae Sigmodontinae Arvicolinae	deer mouse prairie vole meadow vole muskrat	Peromyscus maniculatus Microtus ochrogaster Microtus pennsylvanicus Ondatra zibethicus	2.2.7 2.2.8 2.2.9 2.2.10
Leporidae	eastern cottontail	Sylvilagus floridanus	2.2.11

2.2.1. Short-Tailed Shrew (shrews)

Order Insectivora, Family Soricidae. Shrews are small insectivorous mammals that inhabit most regions of the United States. They have high metabolic rates and can eat approximately their body weight in food each day. Most species are primarily vermivorous and insectivorous, but some also eat small birds and mammals.

Selected species

The northern short-tailed shrew (*Blarina brevicauda*) ranges throughout the north-central and northeastern United States and into southern Canada (George et al., 1986). It eats insects, worms, snails, and other invertebrates and also may eat mice, voles, frogs, and other vertebrates (Robinson and Brodie, 1982). Because they prey on other vertebrates, shrews can concentrate DDT (and presumably other bioaccumulative chemicals) to levels 10 times higher than either *Peromyscus* and *Clethrionomys* (Dimond and Sherburne, 1969). Shrews are an important component of the diet of many owls (Palmer and Fowler, 1975; Burt and Grossenheider, 1980) and are also prey for other raptors, fox, weasels, and other carnivorous mammals (Buckner, 1966).

Body size. Short-tailed shrews are 8 to 10 cm in length with a 1.9 to 3.0 cm tail (Burt and Grossenheider, 1980). The short-tailed shrew is the largest member of the genus, with some weighing over 22 g (George et al., 1986; see table). Some studies have found little or no sexual dimorphism in size (Choate, 1972), while other reports show that males are slightly larger than females (George et al., 1986; Guilday, 1957).

Metabolism. Short-tailed shrews are active for about 16 percent of each 24-hour period (Martinsen, 1969), in periods of around 4.5 minutes at a time (Buckner, 1964). The shrew's metabolism is inversely proportional to the ambient temperature, within the range of 0 to 25°C (Randolph, 1973). Sleeping metabolism is half that associated with normal, exploring activity (Randolph, 1973). Randolph (1973) developed a regression equation for metabolism (cc O₂/g-hour) during (1) interrupted sleep:^e

```
(Winter) Y = 4.754 - 0.0869 (X - 16.4305)
(Summer) Y = 5.3448 - 0.1732 (X - 16.2310)
```

and (2) normal exploring activity:

```
(Winter) Y = 6.5425 - 0.0516 (X - 12.0600)
(Summer) Y = 7.949 - 0.2364 (X - 16.9554) where X = ambient temperature in °C.
```

Randolph (1973) also developed a regression equation for overall metabolism (cal/animal-hour) for shrews spending equal amounts of time sleeping and exploring (cal/animal-hour) as a function of ambient temperature:

^{*}Randolph's (1973) equations could be simplified to match that of Deavers and Hudson (1981; next page) in form; however, we report the equations as Randolph reported them.

```
(Winter) Y = 583.83 - 7.53 (X - 13.68)
(Summer) Y = 544.86 - 20.37 (X - 16.33), where X = ambient temperature in ^{\circ}C.
```

Deavers and Hudson (1981) found a linear increase in standard (near basal) metabolism with decreasing temperature that is similar to that for interrupted sleep described above (Y = standard metabolism in cc O_2 /g-hour):

```
Y = 8.84 - 0.22 (X) where X = ambient temperature.
```

Deavers and Hudson (1981) found that within the thermoneutral zone, the standard metabolic rate of the short-tailed shrew is approximately 190 percent the metabolic rate predicted from body weight.

Habitat. Short-tailed shrews inhabit a wide variety of habitats and are common in areas with abundant vegetative cover (Miller and Getz, 1977). Short-tailed shrews need cool, moist habitats because of their high metabolic and water-loss rates (Randolph, 1973).

Food habits. The short-tailed shrew is primarily carnivorous. Stomach analyses indicate that insects, earthworms, slugs, and snails can make up most of the shrew's food, while plants, fungi, millipedes, centipedes, arachnids, and small mammals also are consumed (Hamilton, 1941; Whitaker and Ferraro, 1963). Small mammals are consumed more when invertebrates are less available (Allen, 1938; Platt and Blakeley, 1973, cited in George et al., 1986). Shrews are able to prey on small vertebrates because they produce a poison secretion in their salivary glands that is transmitted during biting (Pearson, 1942, cited in Eadie, 1952). The short-tailed shrew stores food, especially in the autumn and winter (Hamilton, 1930; Martin, 1984). Robinson and Brodie (1982) found that short-tailed shrews cached most (86.6 percent) of the prey captured; only 9.4 percent was consumed immediately. Short-tailed shrews consume approximately 40 percent more food in winter than in summer (Randolph, 1973). The shrew must consume water to compensate for its high evaporative water loss, despite the fact that it obtains water from both food and metabolic oxidation (Chew, 1951). Deavers and Hudson (1981) indicated that the shorttailed shrew's evaporative water loss increases with increasing ambient temperature even within its thermoneutral zone. Short-tailed shrews' digestive efficiency is about 90 percent (Randolph, 1973).

Temperature regulation and molt. The short-tailed shrew does not undergo torpor but uses nonshivering thermogenesis (NST) to compensate for heat loss during cold stress in winter (Zegers and Merritt, 1987). The short-tailed shrew exhibits three molts. Two are seasonal molts, the first in October/November replaces summer with winter pelage and occurs in first- and second-year shrews. The spring molt can occur any time from February to October. The third molt occurs in postjuveniles that have reached adult size (Findley and Jones, 1956).

Breeding activities and social organization. The short-tailed shrew probably breeds all year, including limited breeding in winter even in the northern portions of its range (Blus, 1971). In Illinois, males were found to be most active from January to July, females from March to September (Getz, 1989). There are two peak breeding periods, in

the spring and in late summer or early fall (Blair, 1940). The home ranges of short-tailed shrews in summer overlap both within and between sexes (Blair, 1940), although females with young do exhibit some territoriality (Platt, 1976). Nomadic shrews are either young of the year or adults moving to areas with more abundant prey (Platt, 1976).

Home range and resources. Short-tailed shrews inhabit round, underground nests and maintain underground runaways, usually in the top 10 cm of soil, but sometimes as deep as 50 cm (Hamilton, 1931; and Jameson, 1943, cited in George et al., 1986). Winter, nonbreeding home ranges can vary from 0.03 to 0.07 ha at high prey densities to 1 to 2.2 ha during low prey densities with a minimum of territory overlap. In the summer, ranges of opposite sex animals overlap, but same sex individuals do not; females with young exclude all others from their area (Platt, 1976).

Population density. Population densities vary by habitat and season (Getz, 1989; Jackson, 1961; Platt, 1968). In east-central Illinois, population density was higher in bluegrass than in tallgrass or alfalfa (Getz, 1989). In all three of these habitats, the short-tailed shrew exhibited annual abundance cycles, with peak densities ranging from 2.5 to 45 shrews per hectare, depending on the habitat (Getz, 1989). The peaks occurred from July to October (12.9/ha average for all three habitats), apparently just following peak precipitation levels (Getz, 1989).

Population dynamics. Winter mortality up to 90 percent has been reported for the short-tailed shrew (Barbehenn, 1958; Gottschang, 1965; Jackson, 1961, cited in George et al., 1986); however, Buckner (1966) suggests that mortality rates in winter may be closer to 70 percent, which is similar to the average monthly mortality rate he found for subadult animals. Several litters, averaging four to five pups, are born each year (George et al., 1986).

Similar species (from general references)

- The masked shrew (*Sorex cinereus*) (length 5.1 to 6.4 cm; weight 3 to 6 g) is smaller than the short-tailed shrew and is the most common shrew in moist forests, open country, and brush of the northern United States and throughout Canada and Alaska. It feeds primarily on insects.
- Merriam's shrew (Sorex merriami) (5.7 to 6.4 cm) is found in arid areas and sagebrush or bunchgrass of the western United States and is smaller than the short-tailed shrew.
- The smokey shrew (*Sorex fumeus*) (6.4 to 7.6 cm; 6 to 9 g), smaller than the short-tailed, prefers birch and hemlock forests with a thick leaf mold on the ground to burrow in. It uses burrows made by small mammals or nests in stumps, logs, and among rocks. Range is limited to the northeast United States and east of the Great Lakes in Canada.
- The southeastern shrew (*Sorex longirostris*) (5.1 to 6.4 cm; 3 to 6 g) prefers moist areas. Found mostly in open fields and woodlots, its range is limited

to the southeastern United States. It nests in dry grass or leaves in a shallow depression.

- The long-tailed shrew (Sorex dispar) (7.0 cm; 5 to 6 g) inhabits cool, moist, rocky areas in deciduous or deciduous-coniferous forests of the northeast, extending south to the North Carolina and Tennessee border.
- The vagrant shrew (Sorex vagrans) (5.9 to 7.3 cm; 7 ± g) inhabits marshy wetlands and forest streams. Its range is confined to the western United States, excluding most of California and Nevada. In addition to insects, it also eats plant material.
- The Pacific shrew (Sorex pacificus) (8.9 cm) is slightly larger than the shorttailed shrew. It is limited to redwood and spruce forests, marshes, and swamps of the northern California and southern Oregon coasts.
- The dwarf shrew (*Sorex nanus*) (6.4 cm) is rare throughout its limited range in the western United States.
- The least shrew (Cryptotis parva) (5.6 to 6.4 cm; 4 to 7 g) is easily
 distinguished from other shrews by its cinnamon color. It inhabits grassland
 and marsh; its range is similar to the short-tailed shrew but does not extend
 as far north.
- The desert shrew (*Notiosorex crawfordi*) (Gray shrew) (5.1 to 6.6 cm) is rarely seen and is found only in the arid conditions, chaparral slopes, alluvial fans, and around low desert shrubs of the extreme southwest. It nests beneath plants, boards, or debris.

General references

Burt and Grossenheider (1980); George et al. (1986).

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI)	Location	Reference	Note No.
Body Weight (g)	АВ	15.0 ± 0.78 SD		New Hampshire	Schlesinger & Potter, 1974	
(9)	M summer F summer M fall M fall	19.21 ± 0.42 SD 17.40 ± 0.48 SD 16.87 ± 0.21 SD 15.58 ± 0.23 SD	17.0 - 22.0 14.0 - 21.0 13.0 - 22.0 12.5 - 22.5	w Pennsylvania	Guilday, 1957	
	neonate		0.67 - 1.29	Maryland/lab	Blus, 1971	
Metabolic Rate (IO,/kg-day)	basal average daily	82 125	80 - 84 106 - 150	Pennsylvania/lab	Pearson, 1947	1
(io ₂ ng day)	average daily	127 ± 15.3 SD	94 - 218	NS/lab	Morrison, 1948	2
	+ 20°C - 20°C	126.5 207.1		Ontario, CAN/lab	Randolph, 1973	
Metabolic Rate (kcal/kg-day)	basal average daily	390 600		Pennsylvania/lab	Pearson, 1947	3
	average daily	680		Wisconsin/lab	Morrison et al., 1957	4
Food Ingestion Rate	A B: 22 - 23°C	7.95 ±0.17 g/d SD 0.49 g/g-day 0.62 g/g-day		Ohio/lab	Barrett & Stuek, 1976	5
	A B: 25°C	0.02 g/g day		Wisconsin/lab	Morrison et al., 1957	6
Water Ingestion Rate (g/g-day)	АВ	0.223		Illinois/lab	Chew, 1951	
Inhalation Rate (m³/day)	АВ	0.026			estimated	7
Surface Area (cm²)	АВ	54		Pennsylvania/lab	Pearson, 1947	8
. ,	AB	84			estimated	9

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
earthworms slugs & snails misc. animals Endegon (fungi) beetles vegetation lepidopteran larvae chilopoda other		31.4 27.1 8.1 7.7 5.9 5.4 4.3			New York/NS (% volume; stomach contents) (June through October collections combined)	Whitaker & Ferraro, 1963	
insects annelids vegetable matter centipedes arachnids snails small mammals crustacea undetermined		77.6 41.8 17.1 7.4 6.1 5.4 5.2 3.7 2.4			eastern United States (primarily New York)/NS (% frequency of occurrence; stomach contents) (all seasons combined)	Hamilton, 1941	
Population Dynamics	Age/Sex/ Cond./Seas.	Mean		Range	Location/Habitat	Reference	Note No.
Home Range Size (ha)	A F summer A M summer			< 0.1 - 0.36 < 0.1 - 1.8	s Michigan/bluegrass	Blair, 1940	
	B B all B B winter (a) B B winter (b)	0.39 ± 0.036 S	SD.	0.03 - 0.07 0.10 - 0.22	s Manitoba/tamarack bog	Buckner, 1966 Platt, 1976	10

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Population Density (N/ha)	winter spring summer fall	2.3 5.9 11.4 10.0		ec Illinois/alfalfa	Getz, 1989	
		10.0	1.6 - 121	Wisconsin/beech-maple	Jackson, 1961; Williams,	11
	ВВ		0.06 - 0.16	Manitoba, Canada/ tamarack bog	Buckner, 1966	
Litter Size		5.4	2 - 8	Indiana/NS	French, 1984	
J		4.7 ± 0.2 SE	1 - 8	Maryland/lab	Blus, 1971	
Litters /Year		several		NS/NS	George et al., 1986	
Days Gestation		21 - 22		Maryland/lab	Blus, 1971	12
Age at Weaning (days)		25 - 30		Maryland/lab	Blus, 1971	
Age at Sexual	М		<u>></u> 65 days	Maryland/lab	Blus, 1971	
Maturity	М		≥ 83 days	NS/NS	Pearson, 1944	11
	F	< 1 year		Indiana/NS	French, 1984	
Annual Mortality	ВВ	93 %		MD, PA, NY, MA/NS	Pearson, 1945	
Longevity	M F	4.6 months 4.4 months		Maryland/lab	Blus, 1971	13
	В		< 20 months	c New York/woods, field	Dapson, 1968	

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Short-Tailed Shrew

Season Activit		Begin	Peak	End	Location	Reference	Note No.
Mating		late February	April - May	mid-September	Indiana	French, 1984	
Parturi	ition		May - June		c New York	Dapson, 1968	
Molt	fall spring	October February		November July	NS NS	Findley & Jones, 1956 Findley & Jones, 1956	11 11

- 1 Ambient temperatures 25 to 30°C; mean weight of shrews = 21.2 g.
- 2 Ambient temperatures 15 to 25 °C; mean weight of shrews = 21 q.
- 3 Calculated from oxygen consumption rate; mean weight of shrews = 21.2 g. Basal metabolism is 186 percent higher than predicted from equations 3-42 or 3-43, in agreement with the finding of Deavers and Hudson (1981). Average daily metabolism was estimated over 24-hour period at 25 to 30°C and is 146 percent higher than the free-living metabolic rate predicted on the basis of equation 3-47 (Nagy, 1987).
- 4 Calculated from average food consumption rate (liver; 1.22 kcal/g wet weight) at 25 °C. This value is 167 percent higher than the free-living metabolic rate predicted on the basis of equation 3-47 (Nagy, 1987).
- 5 Diet of mealworms estimated to provide 2.33 kcal/g live weight. Assimilation efficiency for shrews consuming mealworms = 89.5 ± 1.9 SD.
- 6 Diet of beef liver; mean weight of shrews = 21 g.
- 7 Estimated using equation 3-20 (Stahl, 1967) and adult male summer body weights from Guilday (1957).
- 8 Estimate for 21.2-g shrew.
- 9 Estimated using equation 3-22 (Stahl, 1967) and adult male summer body weights from Guilday (1957).
- 10 (a) At high prey density; (b) at low prey density.
- 11 Cited in George et al. (1986).
- 12 From pairing to parturition.
- 13 Mean longevity of animals that survived to weaning.

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2.2.2. Red Fox (foxes and coyotes)

Order Carnivora, Family Canidae. Unlike the more social wolves, foxes and coyotes tend to hunt alone, although coyotes may hunt larger prey in pairs. Foxes and coyotes are primarily carnivorous, preying predominantly on small mammals, but they also may eat insects, fruits, berries, seeds, and nuts. Foxes are found throughout most of the United States and Canada, including the arctic, as are coyotes with the exception of the southeastern United States. Foxes and coyotes are active primarily at night.

Selected species

Red foxes (*Vulpes vulpes*) are present throughout the United States and Canada except in the southeast, extreme southwest, and parts of the central states. Red fox prey extensively on mice and voles but also feed on other small mammals, insects, hares, game birds, poultry, and occasionally seeds, berries, and fruits (Palmer and Fowler, 1975). Twelve subspecies are recognized in North America (Ables, 1974).

Body size. The dog-sized red fox has a body about 56 to 63 cm in length, with a 35 to 41 cm tail (Burt and Grossenheider, 1980). They weigh from 3 to 7 kg, with the males usually outweighing the females by about 1 kg (Voigt, 1987; see table).

Habitat. As the most widely distributed carnivore in the world, the red fox can live in habitats ranging from arctic areas to temperate deserts (Voigt, 1987). Red foxes utilize many types of habitat--cropland, rolling farmland, brush, pastures, hardwood stands, and coniferous forests (MacGregor, 1942; Eadie, 1943; Cook and Hamilton, 1944; Ables, 1974). They prefer areas with broken and diverse upland habitats such as occur in most agricultural areas (Ables, 1974; Samuel and Nelson, 1982; Voigt, 1987). They are rare or absent from continuous stands of pine forests in the southeast, moist conifer forests along the Pacific coast, and semiarid grasslands and deserts (Ables, 1974).

Food habits. The red fox feeds on both animal and plant material, mostly small mammals, birds, insects, and fruit (Korschgen, 1959; Samuel and Nelson, 1982). Meadow voles are a major food in most areas of North America; other common prey include mice and rabbits (Korschgen, 1959; Voigt, 1987). Game birds (e.g., ring-necked pheasant and ruffed grouse) and waterfowl are seasonally important prey in some areas (Pils and Martin, 1978; Sargeant, 1972; Voigt and Broadfoot, 1983). Plant material is most common in red fox diets in summer and fall when fruits, berries, and nuts become available (Johnson, 1970; Major and Sherburne, 1987). Red foxes often cache food in a hole for future use (Samuel and Nelson, 1982). They also are noted scavengers on carcasses or other refuse (Voigt, 1987). Most activity is nocturnal and at twilight (Nowak and Paradiso, 1983).

Temperature regulation and molt. In winter, foxes do not undergo hibernation or torpor; instead, they are active year-round. They undergo one molt per year, which usually begins in April and is finished by June. The winter coat is regrown by October or November in northern latitudes (Voigt, 1987).

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Breeding activities and social organization. Breeding occurs earlier in the south than in the red fox's northern ranges (Samuel and Nelson, 1982) (see table). A mated pair maintains a territory throughout the year, with the male contributing more to its defense than the female (Preston, 1975). Pups are born and reared in an underground den, and the male assists the female in rearing young, bringing food to the den for the pups (Samuel and Nelson, 1982). Pups first emerge from the den when 4 to 5 weeks old (Samuel and Nelson, 1982). Once considered solitary, red foxes now are reported to exhibit more complex social habits (MacDonald and Voigt, 1985). A fox family, the basic social unit, generally consists of a mated pair or one male and several related females (MacDonald, 1980; Voigt, 1987). The additional females are usually nonbreeders that often help the breeding female (Voigt, 1987).

Home range and resources. The home ranges of individuals from the same family overlap considerably, constituting a family territory (Sargeant, 1972; Voigt and MacDonald, 1984). Territories of neighboring red fox families are largely nonoverlapping and contiguous, usually resulting in all parts of a landscape being occupied by foxes. Territory sizes range from less than 50 to over 3,000 ha (see table). Territories in urban areas tend to be smaller than those in rural areas (Ables, 1969). Adults visit most parts of their territory on a regular basis; however, they tend to concentrate their activities near to their dens, preferred hunting areas, abundant food supplies, and resting areas (Ables, 1974; Keenan, 1981). Territory boundaries often conform to physical landscape features such as well-traveled roads and streams (Ables, 1974). Territory defense is primarily by nonaggressive mechanisms involving urine scent-marking and avoidance behaviors. Scent marking occurs throughout the territory; there is little patrolling of territory boundaries. Each fox or family usually has a main underground den and one or more other burrows within the home range (Nowak and Paradiso, 1983). Most dens are abandoned burrows of other species (e.g., woodchucks, badgers) (Samuel and Nelson, 1982). Tunnels are up to 10 m in length and lead to a chamber 1 to 3 m below the surface (Nowak and Paradiso, 1983). Pup-rearing dens are the focal point of fox activity during spring and early summer. Foxes have some rest sites and usually forage away from the den (Voigt, 1987).

Population density. One red fox family per 100 to 1,000 ha is typical (Voigt, 1987; see table). Red foxes have larger home ranges where population densities are low and in poorer habitats (Voigt, 1987). Most young foxes, especially males, disperse before the age of 1 (Voigt, 1987), usually during September to March, with peaks in dispersal in October and November (Phillips et al., 1972; Storm et al., 1976).

Population dynamics. Foxes usually produce pups their first year, except in extremely high density areas and in some years in northern portions of their range where they may delay breeding until the next season (Allen, 1984; Harris, 1979; Storm et al., 1976; Voigt and MacDonald, 1984). Litter size generally averages four to six pups (see table). The pups leave the den about 1 month after birth, and they are weaned by about 8 to 10 weeks of age (Ables, 1974). Red foxes incur high mortality rates as a result of shooting, trapping, disease, and accidents (e.g., roadkills) (Storm et al., 1976). Two factors that tend to limit red fox abundance are competition with other canids, especially coyotes, and seasonal limits on food availability (Voigt, 1987). Fecundity is higher in areas of high mortality and low population densities (Voigt, 1987).

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Similar species (from general references)

- The arctic fox (*Alopex lagopus*) is smaller than the red fox (body length approximately 51 cm; weight 3.2 to 6.7 kg) and is restricted in its distribution to the arctic, found in the United States only in Alaska. This species primarily scavenges for food but also eats lemmings, hares, birds, and eggs as well as berries in season.
- The swift fox (*Vulpes velox*) is smaller than the red fox (body length 38 to 51 cm; weight 1.8 to 2.7 kg) and inhabits the deserts and plains of the southwest and central United States. It dens in ground burrows and feeds on small mammals and insects.
- The kit fox (*Vulpes macrotis*) is similar in size to the swift fox and is considered by some to be the same species, although it has noticeably larger ears. It inhabits the southwestern United States and prefers open, level, sandy areas and low desert vegetation. It feeds on small mammals and insects.
- The gray fox (*Urocyon cinereoargenteus*) is similar in size (body length 53 to 74 cm; weight 3.2 to 5.8 kg) to the red fox and ranges over most of the United States except the northwest and northern prairies, inhabiting chaparral, open forests, and rimrock regions. Secretive and nocturnal, gray foxes will climb trees to evade enemies. They feed primarily on small mammals but also eat insects, fruits, acorns, birds, and eggs.
- The coyote (Canis latrans) is much larger (body length 81 to 94 cm; weight 9 to 22 kg) than the red fox and is found throughout most of the United States (except possibly eastern), western Canada, and Alaska. It inhabits prairies, open woodlands, brushy and boulder-strewn areas, and dens in the ground. Coyotes share some feeding habits with the red fox but also scavenge and hunt larger prey in pairs.

General references

Ables (1974); Burt and Grossenheider (1980); Palmer and Fowler (1975); Voigt (1987).

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Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% Cl of mean)	Location	Reference	Note No.
Body Weight (kg)	A M spring A F spring	5.25 ± 0.18 SE 4.13 ± 0.11 SE	4.54 - 7.04 3.27 - 4.72	Illinois	Storm et al., 1976	
	A M fall A F fall	4.82 ± 0.081 SE 3.94 ± 0.079 SE	4.13 - 5.68 2.95 - 4.59	lowa	Storm et al., 1976	
	neonate B at weaning B	0.102 ± 0.12 SD 0.70	0.071 - 0.109	Wisconsin North Dakota	Storm & Ables, 1966 Sargeant, 1978	
Pup Growth Rate (g/day)	birth to weaning	15.9		North Dakota/lab	Sargeant, 1978	
Metabolic Rate (kcal/kg-day)	J summer	193 ± 56 SD		Ohio/lab	Vogtsberger & Barrett, 1973	
(Kcarky-day)	A M basal A F basal	47.9 51.1			estimated	1
	A M free-living A F free-living	161	(68 - 383)		estimated	2
		168	(71 - 400)			
Food Ingestion Rate (g/g-day)	J 5-8 wks J 9-12 wks J 13-24 wks	0.16 0.12 0.11		North Dakota/lab	Sargeant, 1978	
	A before whelp	0.075		North Dakota/captive	Sargeant, 1978	3
	F after whelp	0.14				
	A nonbreeding	0.069		North Dakota/captive	Sargeant, 1978	
Water Ingestion Rate (g/g-day)	A M A F	0.084 0.086			estimated	4
Inhalation Rate (m³/day)	A M A F	2.0 1.7			estimated	5

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Factors	Age/Sex/ Cond./Seas.	Mean		ange or 5% Cl of mean)	Location	Reference	Note No.
Surface Area (cm²)	A M A F	3,220 2,760				estimated	6
Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
rabbits				44.4	Nebraska/statewide	Powell & Case, 1982	
small mammals				33.0			
pheasant				8.4	(% wet volume; stomach		
other birds				11.2	contents)		
misc.				2.0			
not accounted for	or			1.0			
mammals	92.2	37.1	61.	7 65.0	Illinois/farm and woods	Knable, 1974	
birds	2.4	43.2	0.2	2 8.6		,	
arthropods	0.2	11.6	4.2	2 <0.1			
plants	4.6	6.3	31.	1 26.1	(% wet weight; stomach		
unspecified/othe	er 0.6	1.8	2.8	3 0.3	contents)		
rabbits	24.8	10.7	36.	38.7	Missouri	Korschgen, 1959	
mice/rats	24.2	6.2	21.	3 22.5			
other mammals	4.0	1.4	8.	1 8.2	(% wet volume; stomach		
poultry	21.0	45.0	16.	3 11.6	contents)		
carrion	12.9	13.0	6.	5 7.4	_		
livestock	9.8	0.3	2.0	5.4			
birds	0.6	1.2	1.1	1 3.8			
invertebrates	trace	15.3	1.0	6 trace			
plant foods	2.7	6.9	6.0	6 2.1			
mammals				81.4	Maryland/Appalachian	Hockman & Chapman, 1983	
birds				4.8	Province (fall & winter)		
arthropods				2.8	()		
plants				7.0	(% wet weight; stomach		
unspecified/othe	er			4.0	contents)		

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Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Territory size (ha)	A B summer A M summer A F summer	1,611 1,967 1,137	277 - 3,420 514 - 3,420 277 - 1,870	nw British Columbia/ alpine and subalpine	Jones & Theberge, 1982	
	A F spring	699 ± 137 SD	596 - 855	ec Minnesota/woods, fields,	Sargeant, 1972	
	A M all year A F all year	717 96	57 - 170	Wisconsin/diverse	Ables, 1969	
Population Density (N/ha)	B B spring	0.001		Canada/northern boreal forests/arctic tundra	Voigt, 1987	
zonon y (rama)	B B spring	0.01		s Ontario, Canada/southern habitats	Voigt, 1987	
	ВВ		0.046 - 0.077	"good fox range" in North America	Ables, 1974	
Litter Size		5.5		s Wisconsin/farm, marsh,	Pils & Martin, 1978	7
O.Z.C		6.8	2 - 9	Illinois/farm and woods	Storm et al., 1976	8
		6.7	3 - 12	lowa/farm and woods	Storm et al., 1976	7
		4.2		upper Michigan/NS	Switzenberg, 1950	8
		4.1		North Dakota/prairie potholes	Allen, 1984	7
Litters/Year		1		NS/NS	Samuel & Nelson, 1982	
Days Gestation		51 - 54		New York/NS	Sheldon, 1949	9
Age at Weaning		8 - 10 weeks		NS/NS	Ables, 1974	
Age at Sexual Maturity	F	10 months		Illinois, lowa/farm woods	Storm et al., 1976	

Red Fox (Vulpes vulpes)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Annual Mortality	ВВ	79.4		s Wisconsin/various	Pils & Martin, 1978	
Rates (percent)	JM JF AF AB	83 81 74 77		Illinois/lowa/ farms and woods	Storm et al., 1976	
Longevity		< 1.5 yrs	up to 6 yrs	NS/NS	Storm et al., 1976	
Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	early Dec. late December late January February	late January Jan Feb.	late February March early February March	lowa New York southern Ontario, Canada northern Ontario, Canada	Storm et al., 1976 Layne & McKeon, 1956; Sheldon, 1949 Voigt, 1987 Voigt, 1987	9
Parturition		March late March, April		southern CAN e North Dakota	Voigt, 1987 Sargeant, 1972	
Molt	April		June	NS/NS	Voigt, 1987	
Disperal	late September		March	Illinois, Iowa	Storm et al., 1976	

- 1 Estimated using extrapolation equation 3-45 (Boddington, 1978) and body weights from Storm et al. (1976) (Illinois).
- 2 Estimated using extrapolation equation 3-47 (Nagy, 1987) and body weights from Storm et al. (1976) (Illinois).
- 3 Food consumption of an adult pair for 11 days prior to whelping (i.e., parturition) and of the adult female for the first 4 weeks after whelping.
- 4 Estimated using extrapolation equation 3-17 (Calder and Braun, 1983) and body weights from Storm et al. (1976) (Illinois).
- 5 Estimated using extrapolation equation 3-20 (Stahl, 1967) and body weights from Storm et al. (1976) (Illinois).
- 6 Estimated using extrapolation equation 3-22 (Stahl, 1967) and body weights from Storm et al. (1976) (Illinois).
- 7 Litter size determined from embryo count. Using placental scars generally overestimates litter size, and counting live pups often underestimates litter size (Allen, 1983; Lindstrom, 1981).
- 8 Method of determining litter size not specified.
- 9 Cited in Samuel and Nelson (1982).

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2-232 Red Fox

2.2.3. Raccoon (raccoons, coatis, ringtails)

Order Carnivora, Family Procyonidae. Procyonids are medium-sized omnivores that range throughout much of North America. Raccoons, coatis, and ringtails feed on insects, small mammals, birds, lizards, and fruits. Ringtails are much smaller and more slender than raccoons and consume a higher proportion of animal matter (Kaufmann, 1982). Coatis are slightly smaller than racoons and are limited in their distribution in the United States to just north of the Mexican border.

Selected species

The raccoon (*Procyon lotor*) is the most abundant and widespread medium-sized omnivore in the North America. They are found throughout Mexico, Central America, the United States, except at the higher elevations of the Rocky Mountains, and into southern Canada (Kaufmann, 1982). During the last 50 years, raccoon populations in the United States have increased greatly (Sanderson, 1987). In suburban areas, they frequently raid garbage cans and dumps. Raccoons are preyed on by bobcats, coyotes, foxes, and great horned owls (Kaufmann, 1982). Twenty-five subspecies are recognized in the United States and Canada; however, most researchers do not identify the subspecies studied because different subspecies inhabit essentially nonoverlapping geographic ranges.

Body size. Raccoons measure from 46 to 71 cm with a 20 to 30 cm tail. Body weights vary by location, age, and sex from 3 to 9 kg (Kaufmann, 1982; Sanderson, 1987). The largest raccoons recorded are from Idaho and nearby states, while the smallest reside in the Florida Keys (Lotze and Anderson, 1979). Juveniles do not reach adult size until at least the end of their second year (Stuewer, 1943b). In the autumn, fat reserves account for 20 to 30 percent or more of the raccoon's weight (Whitney and Underwood, 1952, cited in Kaufmann, 1982). In Minnesota, Mech et al. (1968) found that juveniles gained weight almost linearly until mid-November, after which they began to lose weight until April. Weight loss in adults and yearlings can reach 50 percent during the 4 months of winter dormancy (e.g., 4.3-kg loss for a 9.1-kg raccoon) (Thorkelson and Maxwell, 1974; Mech et al., 1968). In Alabama, where raccoons are active all year, winter weight losses are less, 16 to 17 percent on average (Johnson, 1970).

Habitat. Raccoons are found near virtually every aquatic habitat, particularly in hardwood swamps, mangroves, floodplain forests, and freshwater and saltwater marshes (Kaufmann, 1982). They are also common in suburban residential areas and cultivated and abandoned farmlands (Kaufmann, 1982) and may forage in farmyards (Greenwood, 1982). Stuewer (1943a) stated that a permanent water supply, tree dens, and available food are essential. Raccoons use surface waters for both drinking and foraging (Stuewer, 1943a).

Food habits. The raccoon is an omnivorous and opportunistic feeder. Although primarily active from sunset to sunrise (Kaufmann, 1982; Stuewer, 1943a), raccoons will change their activity period to accommodate the availability of food and water (Sanderson, 1987). For example, salt marsh raccoons may become active during the day to take advantage of low tide (Ivey, 1948, cited in Sanderson, 1987). Raccoons feed primarily on fleshy fruits, nuts, acorns, and corn (Kaufmann, 1982) but also eat grains, insects, frogs,

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crayfish, eggs, and virtually any animal and vegetable matter (Palmer and Fowler, 1975). The proportion of different foods in their diet depends on location and season, although plants are usually a more important component of the diet. They may focus on a preferred food, such as turtle eggs, when it is available (Stuewer, 1943a). They also will feed on garbage and carrion. Typically, it is only in the spring and early summer that raccoons eat more animal than plant material. Their late summer and fall diets consist primarily of fruits. In winter, acorns tend to be the most important food, although raccoons will take any corn or fruits that are still available (Kaufmann, 1982; Stuewer, 1943a).

Temperature regulation and molt. From the central United States into Canada, raccoons undergo a winter dormancy lasting up to 4 months (Stuewer, 1943a). It is not a true hibernation, however, and they can be easily awakened (Kaufmann, 1982). Animals in the south are active year-round (Goldman, 1950). Snow cover, more than low temperatures, triggers winter dormancy (Stuewer, 1943a; Mech et al., 1966; Kaufmann, 1982). The raccoon's annual molt begins early in spring and lasts about 3 months (Kaufmann, 1982).

Breeding activities and social organization. Although solitary, adult raccoons come together for a short time during the mating period (Kaufmann, 1982), which begins earlier (January to March) in their northern range than in their southern range (March to June) (Johnson, 1970; Sanderson, 1987). Male and female home ranges overlap freely and each male may mate with several females during the breeding season (Mech et al., 1966; Johnson, 1970; Kaufmann, 1982; Stuewer, 1943a). The most common group of raccoons is a mother and her young of that year. Further north in their range, a family will den together for the winter and break up the following spring (Kaufmann, 1982). Males are territorial toward one another but not toward females; females are not territorial (Fritzell, 1978).

Home range and resources. The size of a raccoon's home range depends on its sex and age, habitat, food sources, and the season (Sanderson, 1987). Values from a few hectares to more than a few thousand hectares have been reported, although home ranges of a few hundred hectares appear to be most common (see Appendix). In general, home ranges of males are larger than those of females, the home range of females with young is restricted, and winter ranges are smaller than ranges at other times of the year for both sexes (Sanderson, 1987). During the winter, raccoons commonly den in hollow trees; they also use the burrows of other animals such as foxes, groundhogs, skunks, and badgers. These sites are used for sleeping during warmer periods. After wintering in one den, the female will choose a new den in which to bear her young (Kaufmann, 1982). Schneider et al. (1971) found that once the cubs leave the den, the family will not use it again that year.

Population density. Population density depends on the quality and quantity of food resources and den sites. Values between 0.005 and 1.5 raccoons per hectare have been reported, although 0.1 to 0.2 per hectare is more common (see Appendix). Populations exceeding one raccoon per hectare have been reported in residential areas (Hoffman and Gottschang, 1977). Although raccoons may prefer tree dens over ground dens, particularly for raising young (Stuewer, 1943a), Butterfield (1954) found high raccoon densities in an area with few tree dens but numerous ground dens.

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Population dynamics. Males generally are not sexually mature by the time of the first regular breeding season following their birth, but they may mature later that summer or fall (Johnson, 1970; Sanderson, 1951). Females may become pregnant in their first year (Johnson, 1970). In a review of several studies, Kaufmann (1982) found that up to 60 percent of both wild and captive females mate and produce litters in their first year. In Illinois and Missouri, Fritzell et al. (1985) found pregnancy rates of yearlings from 38 to 77 percent. After their first year, almost all females breed annually (Fritzell et al., 1985). Females produce only one litter each year, and the female alone cares for the young (Sanderson, 1987; Stuewer, 1943a, 1943b). With some exceptions (Bissonnette and Csech, 1937), larger litter sizes usually occur in the raccoon's northern range (Lotze and Anderson, 1979). Some juveniles of both sexes disperse from the areas where they were born during the fall or winter of their first year, while others stay and raise young within their parents' home range (Stuewer, 1943a). The highest mortality rates occur within the first 2 years; the age structure of populations in Alabama suggests that mortality is higher for subadults than for juveniles (Johnson, 1970).

Similar species (from general references)

- The coati (*Nasua nasua*) is slightly smaller than the raccoon (4 to 6 kg) but with a much longer tail (51 to 64 cm). Ranging throughout Central America from Panama to Mexico (Kaufmann, 1982), the coati is rare in the United States where it inhabits open forests of the southwest, near the Mexican border. It forages primarily for grubs and tubers but also feeds on fruits, nuts, bird eggs, lizards, scorpions, and tarantulas. Coatis roll arthropods on the ground to remove wings and scales.
- The ringtail (*Bassariscus astutus*) is smaller (36 to 41 cm; 0.9 to 1.13 kg) than the raccoon, with a tail equal to its body length. It ranges throughout the southwestern United States into northern California and Oregon, inhabiting chaparral, rocky ridges, and cliffs near water. Ringtails are omnivorous like the raccoon but consume a higher proportion of animal matter, feeding mainly on small mammals, insects, birds, and lizards as well as fruits. They den in caves or crevices along cliffs, hollow trees, under rocks, and in unused buildings. Although ringtails sometimes live in colonies, mated pairs are more common. More nocturnal than the raccoon, the ringtail is only active at dawn and dusk (Kaufmann, 1982).

General references

Burt and Grossenheider (1980); Goldman (1950); Johnson (1970); Kaufmann (1982); Palmer and Fowler (1975); Sanderson (1987).

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Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI)	Location	Reference	Note No.
Body Weight (kg)	A M A F parous A F nulliparous J M J F	7.6 6.4 6.0 5.1 4.8	7.0 - 8.3 5.6 - 7.1 5.1 - 7.1 4.6 - 5.7 4.2 - 5.3	wc Illinois	Sanderson, 1984	
	A M A F	6.76 5.74		Missouri	Nagel, 1943	
	A M A F	4.31 3.67	up to 8.8 up to 5.9	Alabama	Johnson, 1970	
	neonate	0.075		w New York/captive	Hamilton, 1936	
Pup Growth Rate (g/day)	birth to 7 days 8 to 19 days 20 to 30 days 31 to 40 days 41 to 50 days	17 21 11 12 23		w New York	Hamilton, 1936	
	birth to 6 wks 6 to 9 wks 10 to 16 wks	17.8 3.9 29.5		NS/lab	Montgomery, 1969	
Metabolic Rate (IO ₂ /kg-day)	Winter 15-35°C	9.36 ± 1.68 SD		Washington, DC/National Zoo	Mugaas et al., 1984	
Metabolic Rate (kcal/kg-day)	J B A M basal A F basal	304 44.8 46.8		Ohio/lab	Teubner & Barrett, 1983 estimated	1
	A M free-living A F free-living	183 187	(83 - 400) (85 - 408)		estimated	2
Food Ingestion Rate (g/g-day)						3

Factors	Age/Sex/ Cond./Seas.		Mean	Range or (95%	.CI)	Location	Reference	Note No.
Water Ingestion Rate (g/g-day)	AM 0		0.082 0.083	01 (3370		Location	estimated	4
Inhalation Rate (m³/day)	A M A F		2.47 2.17				estimated	5
Surface Area (cm²)	A M A F		3,796 3,414				estimated	6
Dietary Composition		Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
crayfish snails insects reptiles/amphibit fish rodents corn Smilax acorns pokeberry wild cherry blackberries grapes persimmon	ans	37 5 40 6 3 7 0 0 0 0 0 0	8 5 39 5 2 2 1 trace trace trace 17 16 trace 0	3 18 3 trace trace 2 trace 5 17 2 trace 23 11	9 6 12 7 2 8 19 6 17 2 0 0	Maryland/forested bottomland (% wet volume; digestive tract)	Llewellyn & Uhler, 1952	

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
frogs fish birds mammals other/unspecified persimmon corn grapes pokeberry acorns sugar hackberry cherry insects	8.1 1.2 trace 1.7 7.8 0 57.6 0 0 0	trace 0 0 0 6.7 35.8 0 trace 20.5 0 29.5 3.5	0 0 trace 1.4 1.8 57.3 10.0 10.2 4.5 5.4 5.5 0 2.4	0 0 8.4 0 7.2 27.4 25.9 0 0 4.2 18.4 0 trace	Tennessee/NS (% wet volume; digestive tract)	Tabatabai & Kennedy, 1988	
crayfish Mollusca (mussels and oysters) Crustacea (shrimp & crabs) Pisces (goby & cabezon) Annelida (marine worms) Echiurida (worm)	1.6	4.0 44 25 9 20	1.5	1.4	sw Washington/tidewater mudflats (% wet volume; stomach contents)	Tyson, 1950	
fruits insects mammals grains (e.g. corn) earthworms amphibians vegetation reptiles molluscs birds carrion unspecified		37.9 8.2 14.3 14.7 7.2 4.4 6.1 3.0 1.9 1.5 0.2			New York/NS (% wet volume; stomach contents)	Hamilton, 1951	7

				1		
Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Home Range Size	A M spr./sum. A F spr./sum.	2,560 806	670 - 4,946 229 - 1,632	North Dakota/prairie potholes	Fritzell, 1978	8
(ha)	A M May - Dec A F May - Dec	204 108	18.2 - 814 5.3 - 376	Michigan/riparian	Stuewer, 1943a	
	A M all year A F all year	65 ± 18 SE 39 ± 16 SE		Georgia/coastal island	Lotze, 1979	9
Population	NS	1.46		Ohio/residential woods	Hoffman & Gottschang, 1977	
Density (N/ha)	spring	0.17		Lake Erie, Ohio/ Sandusky Bay, marsh	Urban, 1970	10
	spring	0.022		Wisconsin/marsh	Dorney, 1954	
Litter Size	1 to 3 yrs 4 yrs +	3.4 3.8		n Illinois/NS	Fritzell et al., 1985	
		2.43		Alabama/bottomlands, marsh	Johnson, 1970	
Litters /Year		1		most of range/NS	Sanderson, 1987	
Days Gestation		63		North America/NS	Hamilton, 1936; Sanderson, 1987; Stuewer, 1943b	
Age at Weaning (days)		84	63 - 112	NS/lab	Montgomery, 1969	
Age at Sexual	М	15 months		Alabama/NS	Johnson, 1970	
Maturity	F	1 year		IL, MO/NS	Fritzell et al., 1985	
Annual Mortality	АВ	56		Missouri/NS	Sanderson, 1951	11
Rates (percent)	AB JB	38 42		sw lowa/agricultural	Clark et al., 1989	

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Raccoon (Procyon lotor)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Longevity	A B A B	3.1 years 1.8 years		Alabama/NS Missouri/NS	Johnson, 1970 Sanderson, 1951	11
Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	February January	March February	August March	sw Georgia, nw Florida n United States	McKeever, 1958 Johnson, 1970	
Parturition	April April	early April May	May October	Michigan sw Georgia, nw Florida	Stuewer, 1943b McKeever, 1958	
Molt		summer		northern latitudes	Goldman, 1950	
Torpor	late November		March/April	ec Minnesota	Whitney & Underwood, 1952	12

- 1 Estimated using equation 3-43 (Boddington, 1978) and body weights from Nagel (1943).
- 2 Estimated using equation 3-45 (Nagy, 1987) and body weights from Nagel (1943).
- 3 See Chapters 3 and 4 for methods for calculating food ingestion rates from free-living metabolic rate and diet.
- 4 Estimated using equation 3-17 (Calder and Braun, 1983) and body weights from Nagel (1943).
- 5 Estimated using equation 3-20 (Stahl, 1967) and body weights from Nagel (1943).
- 6 Estimated using equation 3-22 (Stahl, 1967) and body weights from Nagel (1943).
- 7 Collections from April through October.
- 8 Measured from April through July.
- Based on radiotracking.
- 10 Average of three methods of estimating density.
- 11 Hunted population.
- 12 Cited in Schneider et al. (1971).

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2.2.4. Mink (mink, weasels, ermine)

Order Carnivora, Family Mustelidae. Although varied in size, most members of this family have long, slender bodies and short legs. Throughout the family, the male is usually larger than the female. The more terrestrial species feed primarily on small mammals and birds. Mustelids that live around lakes and streams feed on aquatic prey such as fish, frogs, and invertebrates (Burt and Grossenheider, 1980).

Selected species

The mink (*Mustela vison*) is the most abundant and widespread carnivorous mammal in North America. Mink are distributed throughout North America, except in the extreme north of Canada, Mexico, and arid areas of the southwestern United States. It is common throughout its range but often overlooked because of its solitary nature and nocturnal activity. Mink are particularly sensitive to PCBs and similar chemicals, and have been found to accumulate PCBs in subcutaneous fat to 38 to 200 times dietary concentrations, depending on the PCB congener (Hornshaw et al., 1983).

Body size. Body size varies greatly throughout the species' range, with males weighing markedly more than females (in some populations, almost twice as much, see table). Males measure from 33 to 43 cm with a 18 to 23 cm tail. Females measure from 30 to 36 cm with a 13 to 20 cm tail (Burt and Grossenheider, 1980). Farm-raised mink tend to be larger than wild mink (letter from R.J. Aulerich, Department of Animal Science, Michigan State University, East Lansing, MI, to Susan Norton, January 7, 1992).

Metabolism. Harper et al. (1978) evaluated the energy requirements of growing farm-raised male mink during a 21-day period when about 20 percent of their total growth would occur. They expressed food intake on the basis of metabolic body size (MBS) instead of body weight (BW) where MBS = BW(kg) $^{0.73}$. Metabolizable energy (ME) requirements were 147.8 \pm 6.06 (kcal/kg_{MBS}-day). Accounting for assimilation efficiency, this corresponded to a gross energy (GE) intake of approximately 203 (kcal/kg_{MBS}-day).

Iversen (1972) found that basal metabolic rate for mink and other mustelids weighing 1 kg or more could be expressed by the equation:

BMR =
$$84.6Wt^{0.78}$$
 (±0.15),

where BMR = basal metabolic rate in kcal/day and Wt = body weight in kilograms. This model reflects the finding that the larger mustelids have a slightly (10 to 15 percent) higher basal metabolic rate than expected for mammals in general. Free-living metabolic rates would be expected to be three to five times higher (see table).

Habitat. Mink are found associated with aquatic habitats of all kinds, including waterways such as rivers, streams, lakes, and ditches, as well as swamps, marshes, and

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^fMustelid species much smaller than 1 kg (i.e., the stoat and weasel) have much higher basal metabolic rates than predicted for mammals in general.

backwater areas (Linscombe et al., 1982). Mink prefer irregular shorelines to more open, exposed banks (Allen, 1986). They also tend to use brushy or wooded cover adjacent to the water, where cover for prey is abundant and where downfall and debris provide den sites (Allen, 1986).

Food habits. Mink are predominantly nocturnal hunters, although they are sometimes active during the day. Shorelines and emergent vegetation are the mink's principal hunting areas (Arnold, 1986, cited in Eagle and Whitman, 1987). Mink are opportunistic feeders, taking whatever prey is abundant (Hamilton, 1936, 1940; Errington, 1954; Sargeant et al., 1973). Mammals are the mink's most important prey year-round in many parts of their range (Eagle and Whitman, 1987), but mink also hunt aquatic prey such as fish, amphibians, and crustaceans and other terrestrial prev such as bird, reptiles, and insects, depending on the season (Linscombe et al., 1982). In marsh habitats in summer, muskrats can be an important food source depending on their population density and vulnerability (e.g., health) (Hamilton, 1940; Sealander, 1943; Errington, 1954). Mink diet also can depend on marsh water level; Proulx et al. (1987) found that with high water levels, mink captured predominantly crayfish and meadow voles, but during periods of low water, the mink preyed on aquatic birds and muskrats deeper in the marsh. Similarly, Errington (1939) found that mink predation on muskrats in the prairie pothole region can increase dramatically in times of drought as the muskrat burrows become more exposed. Also in this region, ducklings and molting adult ducks that frequent shorelines are particularly vulnerable to mink predation (Arnold and Fritzell, 1987; Sargeant et al., 1973). In winter, mink often supplement their diet with fish (Eagle and Whitman, 1987). Females tend to be limited to smaller prey than males, who are able to hunt larger prey such as rabbits and muskrats more successfully (Birks and Dunstone, 1985; Sealander, 1943).

Temperature regulation and molt. In winter, mink do not undergo hibernation or torpor; instead, they are active year-round. Mink replace their summer coat in mid to late fall with a darker more dense coat and molt again in the spring (Eagle and Whitman, 1987; Linscombe et al., 1982).

Breeding activities and social organization. Mating occurs in late winter to early spring (Eagle and Whitman, 1987). Variation in the length of mating season with different subspecies reflects adaptations to different climates (Linscombe et al., 1982). Ovulation is induced by mating, and implantation is delayed (Eagle and Whitman, 1987). Parturition generally occurs in the late spring, and the mink kits are altricial (helpless) at birth (Linscombe et al., 1982). Mink are generally solitary, with females only associating with their young of the year. Female home ranges generally do not overlap with the home ranges of other females, nor do the home ranges of males overlap with each other (Eagle and Whitman, 1987). The home range of a male may overlap the home range of several females, however, particularly during the breeding season (Eagle and Whitman, 1987).

Home range and resources. The home range of mink encompasses both their foraging areas around waterways and their dens. When denning, mink use bank burrows of other animals, particularly muskrats, as well as cavities in tree roots, rock or brush piles, logjams, and beaver lodges (Melquist et al., 1981; Birks and Linn, 1982; Eagle and Whitman, 1987). Individual mink may use several different dens within their home range, males more so than females (Birks and Linn, 1982). Melquist et al. (1981) found that den

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sites in Idaho were 5 to 100 m from the water, and they never observed mink more than 200 m from water. The shape of mink home ranges depends on habitat type; riverine home ranges are basically linear, whereas those in marsh habitats tend to be more circular (Birks and Linn, 1982; Eagle and Whitman, 1987). Home range size depends mostly on food abundance, but also on the age and sex of the mink, season, and social stability (Arnold, 1986; Birks and Linn, 1982; Eagle and Whitman, 1987; Linn and Birks, 1981; Mitchell, 1961). In winter, mink spend more time near dens and use a smaller portion of their home range than in summer (Gerell, 1970, cited in Linscombe et al., 1982). Adult male home ranges are generally larger than adult female home ranges (Eagle and Whitman, 1987), particularly during the mating season when males may range over 1,000 ha (Arnold, 1986).

Population density. Population density depends on available cover and prey. Population densities typically range from 0.01 to 0.10 mink per hectare (see table). In riverine environments, it can be more meaningful to measure densities in terms of number of mink per unit length of shoreline covered rather than in terms of number per hectare.

Population dynamics. Mink reach sexual maturity at 10 months to a year and may reproduce for 7 years, possibly more (Enders, 1952; Ewer, 1973). Female mink can reproduce once per year and usually give birth to their first litters at the age of 1 year (Eagle and Whitman, 1987). Females often live to the age of 7 years in captivity (Enders, 1952).

Similar species (from general references)

- The long-tailed weasel (*Mustela frenata*) is smaller (males 23 to 27 cm, 200 to 340 g; females 20 to 23 cm, 85 to 200 g) than the mink. It is considered beneficial in agriculture because it kills small rodents, but it does not harm poultry. Although it does not range as far north as the mink, the long-tailed weasel does inhabit parts of the southwest.
- The least weasel (*Mustela nivalis*) is smaller than the mink (males 15 to 17 cm, 39 to 63 g; females 14 to 15 cm, 38 to 40 g) and inhabits meadows, fields, and wooded areas. The least weasel feeds extensively on mice and insects. Its habitat is limited to the north central United States and Canada.
- The ermine (Mustela erminea), or shorttail weasel, is smaller (males 15 to 17 cm, 71 to 170 g; females 13 to 19 cm, 28 to 85 g) than the mink. The ermine inhabits woody areas near water and feeds primarily on small mammals. The ermine's range is limited to the northern and western United States and Canada.
- The black-footed ferret (Mustela nigripes) is larger (36 to 46 cm; up to 1.1 kg) than the mink and inhabits western prairies in the United States, although it now is an endangered species. It feeds on prairie dogs and other small animals.

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General references

Burt and Grossenheider (1980); Eagle and Whitman (1987); Hall (1981); Linscombe et al. (1982); Palmer and Fowler (1975).

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Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Weight (g)	A M A M		< 2,300 < 1,400	western races eastern races	Harding, 1934 Harding, 1934	1
	A M spring A F spring	1,734 ± 350 SD 974 ± 202 SD		Michigan (farm-raised)	Hornshaw et al., 1983	
	A M summer J M summer A M fall J M fall	1,040 777 1,233 952		Montana	Mitchell, 1961	
	A F summer J F summer A F fall J F fall	550 533 586 582		Montana	Mitchell, 1961	
	neonate neonate	8.3 ± 1.54 SD	6 - 10	NS Michigan (farm-raised)	Eagle & Whitman, 1987 Hornshaw et al., 1983	
Pup Growth Rate (g/day)	0-30 days; M 31-90 d; M 91-120 d; M 121-150 d; M 151-180 d; M	7.0 21 15 9.0 4.3		NS/(farm-raised)	Wehr et al. (unpublished)	2
	0-30 days; F 31-90 d; F 91-120 d; F 121-150 d; F 151-180 d; F	6.5 13 6.7 1.7 0.6				

Factors	Age/S	Sex/ I./Seas.	Mean	(9		e or CI of mean)	Location	Reference	Note No.
Metabolic Rate (kcal/kg-day)	AFb AMI		96 84					estimated	3
	AFr	anch cage	258				(farm-raised)	Farrell & Wood, 1968b	
		ree-living free-living	258 236		(110 - (121 -	•		estimated	4
Food Ingestion Rate (g/g-day)	AMs	summer	0.13				(captive)	Arnold & Fritzell, 1987	5
rtate (g/g-day)		winter vinter	0.12 ± 0.0048 SE 0.16 ± 0.0075 SE				Michigan (farm-raised)	Bleavins & Aulerich, 1981	6
	AMy	yr-round	0.22	0.22				estimated	7
Water Ingestion Rate (g/g-day)	A F A M A F		0.11 0.099 0.028				(farm-raised)	estimated Farrell & Wood, 1968c	8
Inhalation Rate (m³/day)	A F A M		0.33 0.55				(lailii-laiseu)	estimated	10
Surface Area (cm²)	A F A M		743 1,120					estimated	11
Dietary Composition		Spring	Summer	Fall	I	Winter	Location/Habitat (measure)	Reference	Note No.
ducks other birds eggs muskrats ground squirrels other mammals		5.2 18.8 3.3 42.0 14.2 15.5	32.5 21.6 14.5 2.1 0.5 25.3				Manitoba, Can/aspen parklands of prairie potholes (% dry weight in scats; male mink only)	Arnold & Fritzell, 1987	

Dietary Composition	Spring	Summer	Fall	Wint	er	Location/Habitat (measure)	Reference	Note No.
(habitat/season) trout non-trout fish	52	ear-round) 2 6	(river; ye	56		Michigan/stream, river (% wet weight; stomach	Alexander, 1977	
unidentified fish crustaceans amphibians birds/mammals	1:	2 5		3 4 3 6		contents)		
vegetation unidentified	17	<i>t</i> 4		1				
(sex of mink) muskrat cottontail small mammals large birds small birds snakes frogs fish crayfish				(M) 43 16 5 18 tra 2 10 5 1	(F) 14 12 17 11 ace 2 37 4	Michigan/NS (% volume; stomach contents)	Sealander, 1943	12
frogs mice & rats fish rabbits crayfish				1	4.9 3.9 9.9 0.2 9.3	Missouri/statewide (% dry volume; stomach contents)	Korschgen, 1958	
birds fox squirrels muskrats other					5.6 2.2 1.3 2.7	·		

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Home Range Size	A M A F A F	770 ha	259 - 380 ha 7.8 ha 20.4 ha	North Dakota/prairie potholes Manitoba, Canada/prairie potholes Montana/riverine: heavy vegetation sparse vegetation	Eagle (unpublished) Arnold & Fritzell, 1987 Mitchell, 1961	13
	A M J M A F	2.63 km 1.23 km 1.85 km	1.8 - 5.0 km 1.1 - 1.4 km 1.0 - 2.8 km	Sweden/stream	Gerell, 1970	1
Population Density	A F winter A F winter	0.03 - 0.085 N/ha 0.006 N/ha 0.6 N/km river		Montana/river Michigan/river	Mitchell, 1961 Marshall, 1936	14
Litter Size		4.2	2 - 8 4 - 10	Michigan/(farm-raised) Montana/river North America/NS	Hornshaw et al., 1983 Mitchell, 1961 Hall & Kelson, 1959	
Litters /Year		1		North America/NS	Hall & Kelson, 1959	
Days Gestation		51	39 - 76 40 - 75	North America/NS United States/(farm-raised)	Hall & Kelson, 1959 Enders, 1952	
Age at Weaning	eat meat fully homeothermic	37 days 7 weeks		Louisiana/NS NS/NS	Svilha, 1931 Kostron & Kukla, 1970	14 14
Age at Sexual Maturity	B B	10 months 1 year		United States/(farm-raised) NS/NS	Enders, 1952 Ewer, 1973	15
Longevity	F	7	maximum 10 years maximum 11 years	NS/zoo NS/(farm-raised)	Eisenberg, 1981 Enders, 1952	

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Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating		April March fall		Alaska Montana Florida, Cypress Swamp	Burns, 1964 Mitchell, 1961 Humphrey & Zinn, 1982	14
Parturition	April		June	most areas (except south)	Eagle & Whitman, 1987	
Molt		mid- to late fall		NS	Eagle & Whitman, 1987	

- 1 Cited in Linscombe et al. (1982).
- 2 Cited in NRC (1982).
- 3 Estimated using Iversen's (1972) model and summer body weights from Mitchell (1961); equation 3-43 (Boddington, 1978) and body weights from Mitchell (1961) yield slightly lower estimates (see text).
- 4 Estimated using equation 3-47 (Nagy 1987) and body weights from Mitchell (1961).
- 5 Arnold and Fritzell (1987) estimated that mink require 180 g of prey per day by assuming a male body mass of 1,420 g and using the model of Cowan et al. (1957) derived from measures of prey requirements for captive mink.
- 6 Diet of whole chicken (20 percent), commercial mink cereal (17 percent), ocean fish scraps (13 percent), and beef parts, cooked eggs, and powdered milk. Moisture content of feed = 66.2 percent.
- 7 Estimated using equation 3-47 (Nagy, 1987), summer body weights from Mitchell (1961), and dietary composition of Alexander (1977). See Chapter 4, Figure 4-7 for the calculations.
- 8 Estimated using equation 3-17 (Calder and Braun, 1983) and body weights from Mitchell (1961).
- 9 Diet contained 65 percent water.
- 10 Estimated using equation 3-20 (Stahl, 1967) and body weights from Mitchell (1961).
- 11 Estimated using equation 3-22 (Stahl, 1967) and body weights from Mitchell (1961).
- 12 Collected from fur buyers.
- 13 Cited in Allen (1986).
- 14 Cited in Eagle and Whitman (1987).
- 15 Cited in Eisenberg (1981).

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2.2.5. River Otter

Order Carnivora, Family Mustelidae. Mustelids have long, slender bodies, short legs, and anal scent glands. Throughout the family, the male is usually larger than the female. The more terrestrial species of this family occupy various habitats and feed primarily on small mammals and birds. Mustelids that live around lakes and streams feed primarily on aquatic species such as fish, frogs, and invertebrates (Palmer and Fowler, 1975; Burt and Grossenheider, 1980).

Selected species

The northern river otter (*Lutra canadensis*) historically lived in or near lakes, marshes, streams, and seashores throughout much of the North American continent (Hall, 1981). Currently, many populations along the coastal United States and Canada are stable or increasing, but this species is rare or extirpated throughout much of the midwestern United States (Toweill and Tabor, 1982). The river otter dens in banks and hollow logs. Individuals range over large areas daily, feeding primarily on fish. Although otters have few natural predators, while on land, they may be taken by coyotes, fox, or dogs (Melquist and Hornocker, 1983). Otters clean themselves frequently by rubbing and rolling in any dry surface (Toweill and Tabor, 1982). Otters appear to undergo bradycardia while submerged and can stay underwater for up to 4 minutes (Melquist and Dronkert, 1987). Because of its piscivorous diet and high trophic level, the river otter is a noteworthy indicator of bioaccumulative pollution in aquatic ecosystems (Melquist and Dronkert, 1987).

Body size. River otters measure 66 to 76 cm with a 30 to 43 cm tail. Sexual dimorphism in size is seen among all subspecies (Harris, 1968; van Zyll de Jong, 1972, cited in Toweill and Tabor, 1982), and adult males (5 to 10 kg) outweigh females (4 to 7 kg) by approximately 17 percent (Melquist and Hornocker, 1983; see Table). Full adult weight generally is not attained until sexual maturity after 2 years of age (Melquist and Hornocker, 1983). Along the Pacific Coast, there is some evidence that size decreases from north to south (Toweill and Tabor, 1982).

Metabolism. Iversen (1972) found that basal metabolic rate of otters and other mustelids weighing 1 kg or more could be expressed by the equation:

BMR =
$$84.6Wt^{0.78}$$
 (±0.15),

where BMR = basal metabolic rate in kcal/day and Wt = body weight in kilograms. Free-living metabolic rates would be expected to be three to five times higher (see table).

Habitat. Almost exclusively aquatic, the river otter is found in freshwater, estuarine, and some marine environments all the way from coastal areas to mountain lakes (Toweill and Tabor, 1982). They are found primarily in food-rich coastal areas, such as the lower portions of streams and rivers, estuaries, nonpolluted waterways, the lakes and tributaries that feed rivers, and areas showing little human impact (Mowbray et al., 1979; Tabor and Wight, 1977).

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Food habits. Otters usually are active in the evening and from dawn to midmorning, although they can be active any time of day (Melquist and Hornocker, 1983). The bulk of the river otter's diet is fish; however, otters are opportunistic and will feed on a variety of prey depending on availability and ease of capture. River otters take different fish species according to their availability and how well the fish can escape capture (Loranger, 1981). Depending on availability, otters also may consume crustaceans (especially crayfish), aquatic insects (e.g., stonefly nymphs, aquatic beetles), amphibians, insects, birds (e.g., ducks), mammals (e.g., young beavers), and turtles (Burt and Grossenheider, 1980; Lagler and Ostenson, 1942; Liers, 1951b; Melquist and Hornocker, 1983; Palmer and Fowler, 1975; Toweill and Tabor, 1982). Gilbert and Nancekivell (1982) observed that otters consume more waterfowl in the northerly latitudes than in the south, probably because of the ease of capturing the waterfowl during their molt in the north. Otters probe the bottoms of ponds or streams for invertebrates and may ingest mud or other debris in the process (Liers, 1951b). Otters in captivity required 700-900 g of food daily (Harris, 1968, cited in Toweill and Tabor, 1982).

Temperature regulation and molt. Seasonal patterns in otters are not well understood. Otters are active throughout the year (Toweill and Tabor, 1982), with the most intense activity levels during the winter (Larsen, 1983; Melquist and Hornocker, 1983). They undergo a gradual molt in spring and fall (Melquist and Dronkert, 1987).

Breeding activities and social organization. Adult males are usually solitary; an adult female and two or three pups make up a typical family group (Melquist and Dronkert, 1987). River otters breed in late winter or early spring over a period of 3 months or more. Birth of a litter follows mating by about 1 year; however, implantation is delayed for approximately 10 months, and active gestation lasts only 2 months (Pearson and Enders, 1944, cited in Toweill and Tabor, 1982; Melquist and Dronkert, 1987). Newborn otters are born blind but fully furred and depend on their mother for milk until 3 to 5 months of age (Johnstone, 1978; Liers, 1951b). Family groups disperse about 3 months after the pups are weaned (Melquist and Hornocker, 1983).

Home range and resources. The river otter's home range encompasses the area needed for foraging and reproduction (Melquist and Dronkert, 1987). The shape of the home range varies by habitat type; for example, near rivers or coastal areas, it may be a long strip along the shoreline (measured in kilometers), but in marshes or areas with many small streams, the home range may resemble a polygon (measured in hectares; Melquist and Dronkert, 1987). All parts of a home range are not used equally; instead, several activity centers may be interconnected by a stream or coast (Melquist and Hornocker, 1983). Food has the greatest influence on habitat use, but adequate shelter in the form of temporary dens and resting sites also plays a role (Anderson and Woolf, 1987a; Melquist and Hornocker, 1983). River otters use dens dug by other animals or natural shelters such as hollow logs, logjams, or drift piles (Toweill and Tabor, 1982; Melquist and Dronkert, 1987). Beaver bank dens and lodges accounted for 38 percent of resting sites used by radio-tracked otters in Idaho (Melquist and Hornocker, 1983). River otters appear to prefer flowing water habitats (e.g., streams) over more stationary water (e.g., lakes, ponds) (Idaho study; Melquist and Hornocker, 1983).

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River otters maintain distinct territories within their home ranges: females maintain a feeding area for their families, males for breeding purposes (Toweill and Tabor, 1982). Individuals tend to avoid confrontation through mutual avoidance (Melquist and Hornocker, 1983). Home ranges are most restricted for lactating females (Melquist and Dronkert, 1987). Adult and subadult males have larger, more variable home ranges than females.

Population density. River otter populations show variable spacing in relation to prey density and habitat (Hornocker et al., 1983). This characteristic, along with their secretive habits and use of several den sites, makes it difficult to estimate river otter populations (Melquist and Dronkert, 1987). Population density of otters often is expressed in terms of number per kilometer of waterway or coastline because of their dependence on aquatic habitats. Densities between one otter every kilometer to one otter every 10 km of river or shoreline are typical (see table).

Population parameters. Otters generally are not sexually mature until 2 years of age (Liers, 1951b; Hamilton and Eadie, 1964; Tabor and Wight, 1977; Lauhachinda, 1978). Adult females appear to reproduce yearly in Oregon (based on a pregnancy rate of almost 100 percent; Tabor and Wight, 1977), but Lauhachinda (1978) concluded that they breed every other year in Alabama and Georgia. Litters usually consist of two to three pups, although litters as large as six pups occur (see table). As adults, river otter mortality rates are low, between 15 and 30 percent per year (Lauhachinda, 1978; Tabor and Wight, 1977).

Similar species (from general references)

The sea otter (*Enhydra lutris*) (76 to 91 cm body and 28 to 33 cm tail; weight 13 to 38 kg) inhabits kelp beds and rocky shores from the Aleutian Islands to California. Its diet includes fish, abalones, sea urchins, and other marine animals.

General references

Burt and Grossenheider (1980); Melquist and Dronkert (1987); Palmer and Fowler (1975); Toweill and Tabor (1982).

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Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Weight (kg)	A B A M A F	8.13 ± 1.15 SD 6.73 ± 1.00 SD	5.0 - 15 5.84 - 10.4 4.74 - 8.72	throughout range Alabama, Georgia	Melquist & Dronkert, 1987 Lauhachinda, 1978	1
	Y M Y F	6.36 ± 0.98 SD 5.83 ± 1.82 SD	4.41 - 8.31 3.75 - 7.01			
	A M A F Y M Y F	9.20 ± 0.6 SE 7.90 ± 0.2 SE 7.90 ± 0.4 SE 7.20 ± 0.1 SE		wc Idaho	Melquist & Hornocker, 1983	
	neonate neonate	0.132 0.140 to 0.145		New York Alabama, Georgia	Hamilton & Eadie, 1964 Hill & Lauhachinda, 1981	
Pup Growth Rate (g/day)	10 to 20 days	26.7		NS	Liers, 1951a	2
Metabolic Rate (kcal/kg-day)	A F basal A M basal	44.8 42.6			estimated	3
	A F free-living A M free-living	183 178	(83 - 400) (81 - 391)		estimated	4
Food Ingestion Rate (g/g-day)						5
Water Ingestion Rate (g/g-day)	A F A M	0.082 0.080			estimated	6
Inhalation Rate (m³/day)	A F A M	2.5 2.9			estimated	7
Surface Area (cm²)	A F A M	3,785 4,280			estimated	8

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Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
fish (sucker) (sculpins) (squawfish) (perch) (whitefish) invertebrates birds mammals	100 (52) (40) (5) (22) (21) 2 <1	93 (47) (31) (4) (3) (10) 7 12	97 (17) (38) (1) (7) (24) 10 1	99 (30) (42) (6) (9) (66) 12 <1	wc Idaho/mountain streams and lakes (percent frequency of occurrence in scats) (most of the fish were longer than 30 cm)	Melquist & Hornocker, 1983	NO.
reptiles	0	1	0	0			
invertebrates (aquatic insects) (fr water shrimp) fishes (trout) (sculpin) (sunfish) frog salamander snake birds mammals	41.6 19.6 14.3 91.4 23.7 20.5 47.1 19.6 0.3 0.2 6.7 8.1	44.2 19.2 8.9 92.9 9.8 20.9 72.8 19.2 0.7 0.7 4.1 5.3	33.3 10.7 10.7 100 33.3 21.3 60.0 10.7 1.3 1.3 2.7	26.3 4.0 4.0 100 29.3 25.3 33.3 9.1 1 4.0	nw Montana/ lakes and streams (percent frequency of occurrence in scats)	Greer, 1955	
fish (sunfish) (minnow/carp) (herring) (bass) frogs crayfish dragonfly nymphs birds	97 (31) (52) (49) (26) 3 12 2	69 (31) (0) (38) (0) 6 50 0	98 (80) (17) (10) (5) 11 8 6	99 (52) (44) (40) (14) 16 7 2	nw Illinois/Mississippi River (percent frequency of occurrence in scats)	Anderson & Woolf, 1987b	

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Dietary						Location/Habitat		Note
Composition		Spring	Summer	Fall	Winter	(measure)	Reference	No.
game & pan fish forage fish fish remains amphibians other invertebrat		32 17.6 3.0 16.1 25.8				Michigan/habitat NS (% volume; stomach contents)	Lagler & Ostenson, 1942	
Other invertebrat	.62	23.6						
Population Dynamics	Age/Sex/ Cond./Se		lean	Range		Location/Habitat	Reference	Note No.
Home Range Size (ha or km	AB			400 - 1	,900 ha	Missouri/marsh, streams	Erickson et al., 1984	9
river)	AB			2,900 -	5,700 ha	Colorado (fall-spr)/NS	Mack, 1985	9
	A M A F	I -	00 ha 95 ha			se Texas/coastal marsh	Foy, 1984	9
	yearling I yearling I adult F B B	F 3	3 ± 20 SD km 2 ± 6.2 SD km 1 ± 9.2 SD km 8 ± 7.5 SD km	10 - 78 25 - 40 23 - 50 15 - 39	km km	wc Idaho/river drainage (no trends seen with season)	Melquist & Hornocker, 1983	
Population Density (N/ha or N/km shoreline)	B B A F breed A M breed yearling I	ding 0	.26/km .05/km .019/km .071/km	0.17 - ().37/km	wc Idaho/river drainage	Melquist & Hornocker, 1983	
	ВВ	0	.85/km			se Alaska/coastal - island	Woolington, 1984	9
	ВВ			0.0094	- 0.014 /ha	se Texas/coastal marsh	Foy, 1984	9
	AB	0	.0025/ha			Missouri/marsh, streams	Erickson et al., 1984	9

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Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Litter Size		2.73 ± 0.77 SD 2.68 ± 0.71 SD 2.1 ± 0.7 SD	1 - 4 1 - 4	Maryland/wetlands Alabama, Georgia/NS New York/NS	Mowbray et al., 1979 Hill & Lauhachinda, 1981 Hamilton & Eadie, 1964	10
	1 yr old 2 yr old 3 yr old 4 yr old 5 to 12 yrs old	0.53 ± 0.91 SD 0.87 ± 0.96 SD 1.60 ± 1.42 SD 2.29 ± 1.25 SD 2.67 ± 1.40 SD	0 - 3 0 - 3 0 - 4 1 - 5 0 - 6	Maine/NS	Docktor et al., 1987	11
Litters /Year		1		NS	Trippensee, 1953	
Days Gestation	total		290 - 380	Wisconsin/captive	Liers, 1951b	12
	active	60-63		NS	Lancia & Hair, 1983	13
Age at Weaning			> 90 days	NS	Harris, 1968	
Age at Sexual Maturity	F M	2 yrs 2 yrs		New York/NS	Hamilton & Eadie, 1964	
Annual Mortality Rates (percent)	birth - 1 yr 1 - 2 yrs 2 - 11 yrs	32 54 27		Oregon/NS	Tabor & Wight, 1977	
	A M A F	17.8 20.3		Alabama, Georgia/riverine	Lauhachinda, 1978	
Longevity	AB		< 15 yrs	Alabama, Georgia/riverine	Lauhachinda, 1978	

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River Otter (Lutra canadensis)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	January March winter	March to April	May April spring	Michigan New York AL, FL, GA	Hooper & Ostenson, 1949 Hamilton & Eadie, 1964 Lauhachinda, 1978	14
Parturition	mid-March late March late January		mid-May early April May	Maryland, Chesapeake Bay wc Idaho Alabama	Mowbray et al., 1979 Melquist & Hornocker, 1983 Lauhachinda, 1978	
Dispersal		April to May		wc Idaho	Melquist & Hornocker, 1983	15

- 1 Summary of studies discussed by Hall (1981) and Woolington (1984).
- 2 Cited in Toweill and Tabor (1982).
- 3 Estimated using equation 3-43 (Boddington, 1978) and adult body weights from Lauhachinda (1978).
- 4 Estimated using equation 3-47 (Nagy, 1987) and adult body weights from Lauhachinda (1978).
- 5 See Chapters 3 and 4 for methods of estimating food ingestion rates.
- 6 Estimated using equation 3-17 (Calder and Braun, 1983) and adult body weights from Lauhachinda (1978).
- 7 Estimated using equation 3-20 (Stahl, 1967) and adult body weights from Lauhachinda (1978).
- 8 Estimated using equation 3-22 (Stahl, 1967) and adult body weights from Lauhachinda (1978).
- 9 Cited in Melquist and Dronkert (1987).
- 10 Determined from implanted embryo counts.
- 11 Determined from corpora lutea counts.
- 12 Total gestation period (including preimplantation).
- 13 Active gestation period (postimplantation), cited in Melquist and Dronkert (1987).
- 14 Cited in Toweill and Tabor (1982).
- 15 Dispersal at age 12 to 13 months.

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2.2.6. Harbor Seal (hair seals)

Order Carnivora, Family Phocidae. Seals, sea lions, and walruses are collectively referred to as pinnipeds (Latin for wing-footed). Pinnipeds are divided into three families: otarids (sea lions and fur seals); phocids (hair seals, also called true seals or earless seals); and walruses. Most pinnipeds feed on marine species such as fish, squid, and other invertebrates (Burt and Grossenheider, 1980). Unlike fur seals, which are protected from the cold marine environment by a dense layer of underfur, phocids rely only on a thick blubber layer for insulation (Pierotti and Pierotti, 1980). Phocids include both the smallest (ring seals) and the largest (elephant seals) of the pinnipeds. The geographic range of most phocid species is from the arctic Atlantic and Pacific south to the coasts of Canada and Alaska, although some do inhabit warmer water (Burt and Grossenheider, 1980). Most phocids, with the exception of the elephant seal, do not exhibit the large disparity in size between the sexes, which is characteristic of otarids (sea lions and fur seals) (Burt and Grossenheider, 1980).

Selected species

In North America, harbor seals (*Phoca vitulina*) range from Alaska to Baja California, Mexico, along the Pacific coast (subspecies *richardsi*; Hoover, 1988), and from Newfoundland to eastern Long Island along the Atlantic coast (subspecies *concolor*; Payne and Selzer, 1989). They are one of the most commonly seen pinniped species, in part due to their tendency to inhabit coastal areas (Hoover, 1988). Harbor seals can be found along the Pacific coast on a year-round basis (except during stormy periods in winter), but Atlantic populations winter offshore when coastal ice has formed in their usual haul-out areas (Boulva and McLaren, 1979). The recent increases in harbor seal populations in New England waters appear to be due to a southward dispersal of seals from rookeries in Maine following the termination of a Massachusetts bounty on harbor seals (1962) and the passage of the Marine Mammal Protection Act (1972) (Payne and Schneider, 1984).

The spotted or largha seal (*Phoca largha*) is a closely related species that until recently was considered a subspecies of the harbor seal. It is similar in size, appearance, and feeding habits to the Pacific harbor seal, but it tends to inhabit colder waters along the Pacific coasts (Ashwell-Erickson and Elsner, 1981). In North America, it seldom ventures further south than the northern coast of Alaska (Ashwell-Erickson and Elsner, 1981). The spotted seal requires ice for breeding haul-outs and gives birth about 2 months earlier than the Pacific harbor seal (Ashwell-Erickson and Elsner, 1981; Boulva and McLaren, 1979). The harbor seal, in contrast, breeds on land (Boulva and McLaren, 1979).

Body size. The length and weight of harbor seals vary geographically, but sexually mature adults tend to be about 1.5 m in length and weigh from 65 to 90 kg (Ashwell-Erickson and Elsner, 1981; Pitcher and Calkins, 1979). Harbor seals exhibit some sexual dimorphism, the male being larger (Pitcher and Calkins, 1979). Body length usually is used to measure size because weight can vary substantially with factors such as season, food availability, and molting (Ronald et al., 1982). Newborn pups are around 80 cm long and weigh from 8.6 to almost 15 kg, with females often weighing less than males (Newby, 1973; Pitcher and Calkins, 1979; Rosen, 1989). Harbor seal pups are highly precocial and are

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able to swim within hours of birth (Boulva and McLaren, 1979; Lawson and Renouf, 1987). Seal milk consists of about half fat, and the pups more than double their weight before they are weaned at approximately 30 days (Bigg, 1969a, as cited in Pitcher and Calkins, 1979). Harbor seals continue to grow with age for several years beyond the age of sexual maturity (Boulva and McLaren, 1979; Pitcher and Calkins, 1979). Body fat varies seasonally with food intake, while total body weight and lean body mass increase with age (Ashwell-Erickson and Elsner, 1981). Harbor seals, unlike many other pinnipeds, do not fast for extended periods during the molting period or breeding season (Boulva and McLaren, 1979; Pierotti and Pierotti, 1980).

Habitat. Harbor seals inhabit a variety of environments and are able to tolerate a wide range of temperatures and water salinities (Boulva and McLaren, 1979; Hoover, 1988). In its eastern range, the harbor seal inhabits inlets, islets, reefs, and sandbars (Boulva and McLaren, 1979). In western North America, the harbor seal inhabits tidal mud flats, sand bars, shoals, river deltas, estuaries, bays, coastal rocks, and offshore islets (Johnson and Jeffries, 1977), even ranging up rivers into freshwater areas in search of food (Roffe and Mate, 1984). Harbor seals also inhabit some freshwater lakes (Power and Gregoire, 1978). Habitats used for haul-outs include cobble and sand beaches, tidal mud flats, offshore rocks and reefs, glacial and sea ice, and man-made objects such as piers and log booms (Hoover, 1988).

Food habits. Harbor seals' diet varies seasonally and includes bottom-dwelling fishes (e.g., flounder, sole, eelpout), invertebrates (e.g., octopus), and species that can be caught in periodic spawning aggregations (e.g., herring, lance, squid) (Everitt et al., 1981; Lowry and Frost, 1981; Pitcher and Calkins, 1979; Roffe and Mate, 1984). Harbor seals are opportunistic, consuming different prey in relation to their availability and ease of capture (Pitcher and Calkins, 1979; Pitcher, 1980; Shaffer, 1989). They may move into rivers on a seasonal basis in pursuit of prey (e.g., eulachon in the Columbia River during winter; Brown et al., 1989). They hunt alone or in small groups (Hoover, 1988). Fish species consumed range between 40 and 280 mm, with mean values of between 60 and 180 mm (Brown and Mate, 1983). Recently weaned pups tend to feed on prey that are more easily captured than fish, such as shrimp or other crustaceans (Hoover, 1988; Pitcher and Calkins, 1979). During the breeding and molting seasons, when harbor seals spend more time on land, adults rely on their blubber layer as an additional source of energy (Ashwell-Erickson and Elsner, 1981). During this time, they may be more susceptible to lipophilic contaminants (e.g., PCBs) that may have accumulated in their blubber (Hoover, 1988).

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⁹Studies of harbor seal diet often rely on counts of fish sagittal otoliths found in scats or stomach contents. These otoliths can be identified to the level of species, annuli on the otoliths counted to determine age, and fish weights and lengths estimated from otolith dimensions. However, partial or complete digestion of otoliths, particularly of small fish species, may result in significant underestimates of the proportion of these prey in seal diets, particularly from scat analysis (da Silva and Neilson, 1985; Harvey, 1989). Studies of stomach contents of stranded seals also may present a biased picture of dietary composition due to extended periods of fasting prior to stranding (Selzer et al., 1986).

In general, food consumption by adult seals is highest in winter and lowest in the summer (Ashwell-Erickson and Elsner, 1981; Ashwell-Erickson et al., 1979). Innes et al. (1987) estimated allometric equations for maintenance food ingestion rates (IR; wet-weight biomass) with body weight (BW, kg) for phocids:

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\begin{split} & \text{IR}_{\text{maint}}(\text{kg/day}) = 0.079 \; \text{BW(kg)}^{0.71} & \text{adult (N = 11; r}^2 = 0.84); \\ & \text{IR}_{\text{maint}}(\text{kg/day}) = 0.032 \; \text{BW(kg)}^{1.00} & \text{juveniles (N = 19; r}^2 = 0.68); \text{ and} \\ & \text{IR}_{\text{maint}}(\text{kg/day}) = 0.068 \; \text{BW(kg)}^{0.78} & \text{both adults and juveniles (N = 30; r}^2 = 0.68). \end{split}
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Allometric equations for food ingestion rates of growing animals (IR; wet-weight biomass) with body weight (BW, kg) for phocids also have been estimated (Innes et al., 1987):

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IR_{growth}(kg/day) = 0.0919 \text{ BW}(kg)^{0.84} \text{ adult (N = 11; } r^2 = 0.84); \text{ and}
IR_{growth}(kg/day) = 0.0547 \text{ BW}(kg)^{0.84} \text{ juveniles (N = 19; } r^2 = 0.68).
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Innes et al. (1987) found that growing juvenile phocid seals ingested 1.7 times more biomass per day than a similar-sized growing adult and 1.4 times more than juvenile phocids that were not growing.

Boulva and McLaren (1979) estimated a relationship between body weight and daily food ingestion for harbor seals from eastern Canada:

$$IR_{free-living}(kg/day) = 0.089 BW(kg)^{0.76}$$
 adults (N = 26).

Perez (1990) estimated the average energy value of the harbor seal's diet to be 1.4 kcal/g wet weight. Ashwell-Erickson and Elsner (1981) provide age-specific estimates of food ingestion rates for the closely related spotted seal (see Appendix) and summarize studies in which food ingestion rates for harbor and spotted seals have been estimated.

Temperature regulation and molt. Harbor seals can maintain their heat balance while diving in water as low as 13°C without increased muscle activity or metabolic rate (Ronald et al., 1982). For seals in general, molting is simply part of an ongoing pelage cycle that is influenced by the seal's environment, physiology, and behavior (Ling, 1974). Phocids get an entirely new coat with each annual molt (Ling, 1970), a process that takes about 5 weeks (Scheffer and Slipp, 1944, as cited in Ashwell-Erickson and Elsner, 1981). During their molt, they spend more time hauled and exhibit a slower metabolic rate (e.g., 83 percent of premolt levels), which decreases their food requirements (Ashwell-Erickson and Elsner, 1981). After molting, harbor seals increase their fat reserves (and weight) for the winter and early spring; metabolic rates also might be lowered during this time to conserve energy (Renouf, 1989).

Breeding activities and social organization. The timing of reproduction in harbor seals varies with location. Mating and pupping are initiated earlier in the year in more

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southern latitudes, but within populations, breeding is synchronized (Hoover, 1988; Slater and Markowitz, 1983). Harbor seals may form large breeding aggregations on land in areas where food resources are plentiful (Slater and Markowitz, 1983); however, pupping activities are not restricted to large, discrete rookeries (Pitcher and Calkins, 1979). Mating occurs soon after weaning, which is 3 to 6 weeks after birth (Ashwell-Erickson and Elsner, 1981). It is likely that harbor seals are promiscuous (Pierotti and Pierotti, 1980), although there is some evidence that they are mildly polygynous, with males defending territories at the haul-out sites (Boulva and McLaren, 1979; Perry, 1989; Slater and Markowitz, 1983). Following mating, implantation is delayed for 1.5 to 3 months, during which time the female molts (Bigg, 1969a; Hoover, 1988; Pitcher and Calkins, 1979). At other times of the year, harbor seals also can be found in groups of 30 to 80 in some haul-out areas (Hoover, 1988).

Home range and resources. Harbor seals generally inhabit highly productive coastal areas, with upwelling ocean currents that bring nutrients to the surface supporting abundant marine life (e.g., the California current system, the Gulf of Alaska, and the Gulf of Maine; Ronald et al., 1982). Harbor seals also require adequate places to haul out, and their distribution is influenced by the availability of suitable sites (Boulva and McLaren, 1979). In general, seals stay near particular haul-out sites with only local movements (Brown and Mate, 1983; Pitcher and Calkins, 1979; Slater and Markowitz, 1983). Haul-out patterns are determined by several factors, including weather, tidal pattern, time of day, season, and human proximity (Slater and Markowitz, 1983). Harbor seals are considered fairly sedentary, with individuals showing year-round site fidelity, although some seasonal movement associated with pupping and long-distance movements are recorded (Pitcher and Calkins, 1979; Slater and Markowitz, 1983). Data on likely daily or monthly foraging distances are lacking.

Population density. Harbor seals are found principally in coastal areas within 20 km of shore; they tend to concentrate in estuaries and protected waters (Hoover, 1988). Their distribution is highly patchy, and local population densities in haul-out areas with favorable food resources nearby can be quite high (Pitcher and Calkins, 1979).

Population dynamics. Females are sexually mature by 3 to 5 years of age, whereas males are sexually mature later, at 4 to 6 years of age (Boulva and McLaren, 1979; Pitcher and Calkins, 1979). Females only produce one pup per year (Hoover, 1988). Three major causes of preweaning pup mortality are stillbirth, desertion by the mother, and shark kills (Boulva and McLaren, 1979). Mortality from birth to 4 years of age was estimated to be 74 percent for females and 79 percent for males in one study, after which it remained at about 10 percent per year (Pitcher and Calkins, 1979). Life expectancy for harbor seals is about 30 years (Newby, 1978).

Similar species (from general references)

 The ringed seal (*Phoca hispida*) is smaller (1.4 m length; weight to 90 kg) than the harbor seal and inhabits colder waters. It feeds mainly on marine invertebrates.

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- The harp seal (*Phoca groenlandicus*) (1.8 m; weight to 180 kg) inhabits deep, icy water. It ranges from the Arctic Atlantic south to Hudson Bay; it is only rarely found further south. It feeds on macroplankton and fish.
- The largha or spotted seal (*Phoca largha*) (1.5 m) is a closely related species that until recently was considered a subspecies of the harbor seal. Its characteristics are compared with those of the harbor seal under *Selected species*.
- The ribbon seal (*Phoca fasciata*) (1.6 m; males to 90 kg, females to 76 kg)
 lives near pack ice in the Bering Sea and feeds on bottom invertebrates, fish,
 and octopus and squid.

General references

Ashwell-Erickson and Elsner (1981); Burt and Grossenheider (1980); Hoover (1988); Pitcher and Calkins (1979); Ronald et al. (1982).

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Harbor Seal (Phoca vitulina)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Body Weight (kg)	A M (> 7 yrs) A F (> 7 yrs)	84.6 ± 11.3 SD 76.5 ± 17.7 SD		Gulf of Alaska	Pitcher & Calkins, 1979	
	J M 2 yrs J M 4 yrs J M 6 yrs A M 8 yrs A M 12 yrs A M 16 yrs A M 24 yrs J F 2 yrs J F 4 yrs J F 6 yrs A F 8 yrs A F 12 yrs A F 12 yrs A F 24 yrs	49 70 84 95 110 120 124 40 56 67 76 90 101 112		Aleutian Ridge and Pribilof Islands, Bering Sea, Alaska	Ashwell-Erickson & Elsner, 1981	1
	neonate M neonate F	12.0 ± 0.51 SE 11.5 ± 0.31 SE		Alaska	Pitcher & Calkins, 1979	
	at weaning B	24.0		British Columbia, Canada	Bigg, 1969a	2
Pup Growth Rate (g/day)	birth to weaning M F	520 790		Gulf of St. Lawrence/island marine	Rosen, 1989	
Metabolic Rate (IO ₂ /kg-day)	J B resting A F resting	7.3 6.6		California/lab	Davis et al., 1985	3

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Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% Cl of mean)	Location	Reference	Note No.
Metabolic Rate (kcal/kg-day)	1 to 4 yrs old/ basal	57.5		Bering Sea, Alaska	Ashwell-Erickson & Elsner, 1981	
	A F basal A M basal	24.3 22.4			estimated	4
	A F free-living A M free-living	131 129	(57 - 300) (56 - 296)		estimated	5
Food Ingestion Rate (g/g-day)	АВ	0.05		e Canada/marine	Boulva and McLaren, 1979	
(3,3)	A B A F lact./gest.	0.06 to 0.08 0.10		review of several studies	Ashwell-Erickson & Elsner, 1981	
	J B 1st year	0.13		Bering Sea (1 harbor & 1 spotted seal)	Ashwell-Erickson & Elsner, 1981	
Water Ingestion	АВ	0.0048	0.0028 - 0.0091	seawater ingestion (most water obtained from food)	Depocas et al., 1971	
Rate (g/g-day)	AB	0.064		,	estimated	6
Inhalation Rate (m³/day)	A M A F	18.6 17.2			estimated	7
Surface Area (cm²)	A M A F	19,620 18,380			estimated	8

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Harbor Seal (Phoca vitulina)

Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
walleye pollock	3.7	27.3	32.2	1.3	Washington/	Everitt et al., 1981	
English sole	37.0	0.0	27.0	0	coastal island	,	
shiner perch	0.0	0.0	0.5	63.6			
Pacific herring	0	54.6	3.9	28.6	(% of total otoliths		
Pacific cod	0	0	10.1	0	recovered from scat		
rex sole	37	9.1	2.9	0	samples)		
Pacific tomcod	3.7	0	4.7	0	. ,		
rockfish	3.7	0	4.7	0			
Dover sole	3.7	0	3.4	2.6			
Petrale sole	7.4	0	1.8	0			
other fish	3.8	9.0	8.8	3.9			
octopus		17.6	17.7	30.4	Kodiak Island, Alaska/	Pitcher & Calkins, 1979	
salmon		5.4	0.0	0.0	coastal marine		
capelin		20.3	4.8	5.4			
Pacific cod		6.8	8.1	10.7	(% frequency of occurrence;		
walleye pollock		12.2	9.7	14.3	stomach contents)		
Pacific sandlance		4.1	21.0	0.0	-		
squid & octopus		20			Gulf of Alaska/	Pitcher, 1980	
shrimp, crabs		3.7			coastal marine	·	
herring		6.4					
salmonids		4.4			(% wet volume; stomach		
osmerids		22.5			contents)		
cod, tomcod,		26.0			-		
walleye, pollock					all seasons combined		
other		14.1					

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Foraging Radius (km)	A B A B	5 km 30 to 55 km	unknown unknown	California/Bay Washington/Columbia River	Stewart et al., 1989 Beach et al., 1985	9 10
Population Density (N/ha)	summer	0.0305	0.00394 - 0.0611 highly clumped distrib.	Maine/coastal marine throughout range and habitats	Richardson, 1981 Pitcher and Calkins, 1979	
Litter Size		1		throughout range and habitats	Hoover, 1988	
Litters /Year		1		throughout range and habitats	Hoover, 1988	
Months Gestation		10.5 to 11		NS/NS	FAO Adv. Comm., 1976	11
Age at Weaning	B B	30 days 35 days		e Canada/marine c California/coastal marine	Boulva & McLaren, 1979 Slater & Markowitz, 1983	
Age at Sexual	F M	5.5 ± 0.23 SE	4 - 9 5 - 7	Gulf of Alaska/coastal marine	Pitcher & Calkins, 1979	
Maturity (years)	F M	3 to 4		e Canada/marine	Boulva & McLaren, 1979	
Annual Mortality	АВ	17.5		e Canada/marine	Boulva & McLaren, 1979	12
Rates (percent)	birth to 4 yrs 4 to 5 yrs old 7 to 14 yrs old ≥ 20 yrs old	77/4 yrs 11/yr 8 to 9/yr 14/yr		Gulf of Alaska/coastal marine	Pitcher & Calkins, 1979	
Longevity	A B		< 30	e Pacific/NS	Newby, 1978	
	A M A F		< 26 < 31	Gulf of Alaska/coastal	Pitcher & Calkins, 1979	

Harbor Seal (Phoca vitulina)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	early April	February July	July	Nova Scotia, Canada Mexico Bering Sea	Boulva & McLaren, 1979 Bigg, 1969b Bigg, 1969b	13 13
Parturition	mid-May late April early February late June	mid-June	late June early May September	Tugidak Island, Alaska c California Mexico Canada	Pitcher & Calkins, 1979 Riedman, 1990	
	May August	early June	June September	Washington Washington, Puget Sound	Johnson & Jeffries, 1983	
Molt	early June late June	late July	early September September/October	Scotland Gulf of Alaska	Thompson & Rothery, 1987 Pitcher & Calkins, 1979	14

- 1 Estimated from graph of growth curve.
- 2 Cited in Boulva and McLaren (1979). Weight doubled from birth.
- 3 Juvenile is a yearling; weight 33 kg. Adult female weight 63 kg.
- 4 Estimated using equation 3-43 (Boddington, 1978) and body weights from Pitcher and Calkins (1979). Caution must be used, however, because pinnipeds were not included in the data set from which the allometric model was derived.
- 5 Estimated using equation 3-47 (Nagy, 1987) and body weights from Pitcher and Calkins (1979). Caution must be used, however, because pinnipeds were not included in the data set from which the allometric model was derived. Mean values are somewhat higher than is consistent with food ingestion rate estimates and data from the spotted seal (see Appendix).
- 6 Estimated using equation 3-17 (Calder and Braun, 1983) and body weights from Pitcher and Calkins (1979). Caution must be used, however, because pinnipeds were not included in the data set from which the allometric model was derived.
- 7 Estimated using equation 3-20 (Stahl, 1967) and body weights from Pitcher and Calkins (1979). Caution must be used, however, because pinnipeds were not included in the data set from which the allometric model was derived.
- 8 Estimated using equation 3-22 (Stahl, 1967) and body weights from Pitcher and Calkins (1979). Caution must be used, however, because pinnipeds were not included in the data set from which the allometric model was derived.
- 9 Satellite telemetry of one seal. Foraging radius depends on distribution and abundance of prey.
- 10 Seventy-five percent of 58 seals radio-tagged in the Columbia River were relocated at haul-out sites 30 to 55 km away. Cited in Hoover (1988).
- 11 Cited in Ronald et al. (1982).
- 12 Postweaning mortality.
- 13 Cited in Hoover (1988).
- 14 Nineteen to 33 days to complete molt.

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2.2.7. Deer Mouse (deer and white-footed mice)

Order Rodentia, Family Muridae (Genus Peromyscus). New world mice (family Muridae) are small, ground-dwelling rodents that live in a large variety of habitats including woodlands, prairies, rocky habitats, tundra, and deserts. All are nocturnal and are preyed on by owls, hawks, snakes, and carnivorous mammals. Most species eat primarily seeds, but some also regularly eat small invertebrates. Many species store food. The genus Peromyscus is the most widespread and geographically variable of North American rodents (MacMillen and Garland, 1989).

Selected species

The deer mouse (*Peromyscus maniculatus*) is primarily granivorous and has the widest geographic distribution of any *Peromyscus* species (Millar, 1989; Brown and Zeng, 1989). It is resident and common in nearly every dry-land habitat within its range, including alpine tundra, coniferous and deciduous forest, and grasslands as well as deserts. There are many recognized subspecies or races of the deer mouse associated with different locations or insular habitats, including *artemisiae*, *austerus*, *bairdii*, *balaclavae*, *blandus*, *borealis*, *carli*, *cooledgei*, *gambelii*, *gracilis*, *labecula*, *maniculatus*, *oreas*, *nebrascensis*, *nubiterrae*, *rufinus*, and *sonoriensis* (MacMillen and Garland, 1989; Millar, 1982)

Body size. Deer mice range from 7.1 to 10.2 cm in length, with a 5.1 to 13 cm tail, and adults weigh from 15 to 35 g (Burt and Grossenheider, 1980; see table). Body size varies somewhat among populations and subspecies throughout the species' range. Body weight also varies seasonally, being lower in autumn and winter and a few grams higher in spring and summer (Zegers and Merritt, 1988). There may (Fleharty et al., 1973) or may not (Millar and Schieck, 1986) be seasonal differences in fat content.

Habitat. Deer mice inhabit nearly all types of dry-land habitats within their range: short-grass prairies, grass-sage communities, coastal sage scrub, sand dunes, wet prairies, upland mixed and cedar forests, deciduous forests, ponderosa pine forests, other coniferous forests, mixed deciduous-evergreen forests, juniper/piñon forests, and other habitats (Holbrook, 1979; Kaufman and Kaufman, 1989; Ribble and Samson, 1987; Wolff and Hurlbutt, 1982). Few studies have found microhabitat features that distinguish the deer mouse, and some studies have come to different conclusions regarding habitat structure preferences (Ribble and Samson, 1987). For example, Vickery (1981) found that deer mice appeared to prefer areas with moderate to heavy ground and mid-story cover to more open ground areas, whereas others have found more deer mice in more open than in more vegetated areas (see Kaufman and Kaufman, 1989).

Food habits. Deer mice are omnivorous and highly opportunistic, which leads to substantial regional and seasonal variation in their diet. They eat principally seeds, arthropods, some green vegetation, roots, fruits, and fungi as available (Johnson, 1961; Menhusen, 1963; Whitaker, 1966). The nonseed plant materials provide a significant

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hPeromyscus is considered a member of the family Cricetidae by some mammalogists.

proportion of the deer mouse's daily water requirements (MacMillen and Garland, 1989). Food digestibility and assimilation for most of their diet have been estimated to be as high as 88 percent (Montgomery, 1989). Deer mice may cache food during the fall and winter in the more northern parts of their range (Barry, 1976; Wolff, 1989). They are nocturnal and emerge shortly after dark to forage for several hours (Marten, 1973).

Temperature regulation. The deer mouse has a metabolic rate about 1.3 times higher than the other species in the genus (MacMillen and Garland, 1989; Morris and Kendeigh, 1981; see table). Its metabolic rate is substantially higher in winter than in summer (Morris and Kendeigh, 1981; Stebbins, 1978; Zegers and Merritt, 1988). Outside the thermoneutral zone (25 to 35°C), metabolic rate varies according to the following equation:

$$V_{02} = 0.116 - 0.003(T_a) + 0.0304 (V^{0.5})$$

where V_{02} = volume oxygen consumed (ml/g-min); T_a = ambient temperature; and V = wind speed (Chappell and Holsclaw, 1984). Deer mice can enter torpor (body temperature, 19 to 30°C) to reduce metabolic demands in the winter and also in response to brief food shortages (Tannenbaum and Pivorun, 1988, 1989). The deer mouse uses nonshivering thermogenesis (NST) to quickly awaken from torpor and to maintain body temperature during the winter (Zegers and Merritt, 1987). The deer mouse may burrow in soils to assist thermoregulation; one study measured the burrow dimensions to be 24 cm deep (range 13 to 50 cm) and 132 cm long (range 30 to 470 cm) (Reynolds and Wakkinen, 1987).

Breeding activities and social organization. The duration of the reproductive season varies with latitude and longitude according to the regression equation:

$$Y = -33.0 + 2.79 X + 0.0748 Z - 0.0370 X^{2}$$

where Y = duration of the breeding season in weeks, X = latitude, and Z = longitude (r = 0.58; Millar, 1989). Lactating females have longer gestation periods than nonlactating females. Newborn deer mice are highly altricial (Layne, 1968). Several studies have indicated that daily food consumption increases over 15 percent during early pregnancy and more than doubles during lactation (Glazier, 1979; Millar, 1975, 1978, 1979, 1982, 1985; Millar and Innes, 1983; Stebbins, 1977). Deer mice are promiscuous; in one study, 19 to 43 percent of litters resulted from multiple inseminations (Birdsall and Nash, 1973, as cited in Millar, 1989).

Home range and resources. Deer mice tend to occupy more than one nest site, most frequently in tree hollows up to 8 m from the ground (Wolff and Durr, 1986) but also among tree roots and under rocks and logs (Wolff and Hurlbutt, 1982; Wolff, 1989). At low densities, home ranges are maintained by mutual avoidance, but at higher densities, females may defend a core area or territory (Wolff, 1989). The home range of female deer mice encompasses both their foraging areas and their nests. Male home ranges are larger and overlap the home ranges of many females (Cranford, 1984; Taitt, 1981; Wolff, 1985a, 1986; Wolff et al., 1983).

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Population density. Population density varies considerably over space and time and is often positively correlated with food abundance (Taitt, 1981; Wolff, 1989), moisture content of plants (Bowers and Smith, 1979), and vegetative cover (van Horne, 1982) as well as season (Montgomery, 1989; Taitt, 1985). Interspecific competition also can play a role in determining population densities (Kaufman and Kaufman, 1989).

Population dynamics. Although laboratory and field studies have demonstrated that females can produce their first litter by 3 months of age, females of the more northern populations do not mature under natural conditions until the spring after the year of their birth. First litters are consistently smaller than subsequent litters (Millar, 1989), and latitude and elevation explain a significant amount of the variation in litter size among *P. maniculatus* populations (Smith and McGinnis, 1968, as cited in Millar, 1989). Millar (1989) estimated the relationship between litter size and latitude and longitude to be

$$Y = -1.62 + 0.0103X + 0.106Z + 0.0004X^2 - 0.0005Z^2$$

where Y is the mean litter size; X, the latitude; and Z, the longitude. The largest litters are produced in northwestern North America. Pups wean within about 3 weeks, and females may have up to four litters per year in the more southern parts of the species' range (Millar, 1989). Mortality rates are high, and most deer mice live for less than 1 year (Millar and Innes, 1983).

Similar species (from general references)

- The cactus mouse (*Peromyscus eremicus*), almost the same size as the deer mouse (8.1 to 9.1 cm; 17 to 40 g), is found only in low deserts of the extreme southwest and Mexico. It may feed on green vegetation, seeds, and berries and can climb trees for food.
- The California mouse (*Peromyscus californicus*) (9.6 to 11.7 cm; 42 to 50 g) is found in southwestern California and lives among oaks and dense chaparral. It stores acorns in nests made of twigs and sticks.
- The canyon mouse (*Peromyscus crinitus*) (7.6 to 8.6 cm) is limited to the western United States. It lives in rocky canyons and on lava-covered slopes, nesting among rocks.
- The oldfield mouse (*Peromyscus polionotus*), smaller than the deer mouse (4.1 to 6.1 cm), is limited to the extreme southeastern United States, where it inhabits sandy beaches and fields and feeds on seeds and berries. Females may be territorial during the breeding season.
- The white-footed mouse (*Peromyscus leucopus*) is approximately the same size as the deer mouse (9.1 to 10.7 cm; 14 to 31 g). Its range extends north into Canada and west to Arizona but does not extend as far north and west as the deer mouse's range. Like the deer mouse, the white-footed mouse's diet consists mainly of arthropods, seeds, and other vegetation, and it usually nests off the ground. It is most abundant in habitat that includes a

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- canopy, such as brushy fields and deciduous woodlots in northern regions and riparian areas and ravines in prairie and semidesert regions.
- The cotton mouse (*Peromyscus gossypinus*) (9.1 to 11.7 cm; 28 to 51 g) is found in the southeastern United States where it inhabits wooded areas, swampland, stream banks, and field edges. This tree climber nests in trees, under logs, and in buildings.
- The brush mouse (*Peromyscus boylii*) (9.7 to 10.7 cm; 22 to 36 g) is limited to chaparral and rocky areas of the arid and semiarid west and southwest United States. A good climber, it lives under rocks and debris and in crevices. It feeds on pine nuts, acorns, seeds, and berries.

General references

Burt and Grossenheider (1980); Kirkland and Lane (1989); Millar (1985, 1989); Wolff (1989).

Factors	Age/Sex Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Body Weight (g)	A M A F	22 20		North America	Millar, 1989	
	A M A F	15.7 14.8		NS (austerus)	Fordham, 1971	1
	A M A F	22.3 21.1		NS (blandus)	Dewsbury et al., 1980	1
	A B	19.6 ± 0.71 SE		New Hampshire	Schlesinger & Potter, 1974	
	A F nonbreed. A F gestat. A F lactat.	20.3 ± 0.42 SE 31.5 ± 0.43 SE 24.5 ± 0.37 SE		NS (<i>borealis</i>) lab	Millar & Innes, 1983	
	neonate neonate	1.8 1.7 ± 0.02 SE	1.6 - 2.8	North America Alberta, Canada	Millar, 1989 Millar, 1989	
	at weaning at weaning	8.8 9.3 ± 0.10 SE	7.7 - 11.2	North America Northwest Territories, Canada	Millar, 1989 Millar, 1979	
Pup Growth Rate (g/day)	В	0.38 ± 0.01 SE	0.30 - 0.95	Alberta, Canada (nebrascensis)	Millar, 1985	
(0)/	M F	0.27 ± 0.06 SE 0.22 ± 0.05 SE		Alberta, Canada (<i>borealis</i>)	Millar & Innes, 1983	2
Metabolic Rate	F resting	50	40 - 61	North America	MacMillen & Garland, 1989	
(IO ₂ /kg-day)	M avg daily: winter spring summer	138 ± 5.3 SE 102 ± 7.2 SE 75 ± 3.4 SE		Alberta, Canada lab	Stebbins et al., 1980	3

Factors	Age/Sex Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
Metabolic Rate (kcal/kg-day)	M avg daily: winter spring summer B free-living: winter summer	668 ± 25 SE 623 ± 35 SE 360 ± 17 SE 790 592		Alberta, Canada lab	Stebbins et al., 1980 Morris & Kendeigh, 1981	3
	A M free-living A F free-living	547 574	(259 - 1,153) (271 - 1,212)		estimated	5
Food Ingestion Rate (g/g-day)	A F nonbreed.	0.19 0.18		Manitoba, Canada (<i>maniculatus</i>) lab Alberta, Canada (<i>borealis</i>) lab	Millar, 1979 Millar & Innes, 1983	6 7 6 7
	A F lactating A F lactating	0.45		Manitoba, Canada (<i>maniculatus</i>) lab Alberta, Canada (<i>borealis</i>) lab	Millar, 1979 Millar & Innes, 1983	8
	A F nonbreed. A M nonbreed.	0.19 0.22		Virginia lab	Cronin & Bradley, 1988	9
	JM	0.21 ± 0.01 SE		South Dakota lab	Nelson & Desjardins, 1987	
Water Ingestion Rate (g/g-day)	AB AB JM	0.19 0.19 0.34 ± 0.02 SE 0.15	0.123 - 0.287	(<i>sonoriensis</i>) lab Illinois (<i>bairdii</i>) lab South Dakota lab	Ross, 1930 Dice, 1922 Nelson & Desjardins, 1987 estimated	10 11 12 13
Inhalation Rate (m³/day)	A M A F	0.025 0.023			estimated	14
Surface Area (cm²)	A M A F	91 86			estimated	15

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Dietary Composition	Spring	Summer	Fall	Winter	Location (subspecies)/Habitat (measure)	Reference	Note No.
nuts/seeds		0	24	23	Virginia (<i>nubiterrae</i>)/	Wolff et al., 1985	
arthropods		56	30	46	oak-maple-hickory forest	,	
Lepidopt. larvae		4	trace	2			
Lepidopt. adults		3	26	7	(% frequency of occurrence;		
green veg.		5	12	18	stomach contents)		
fungus		7	trace	1	•		
fruit		25	4	1			
unknown		1	4	3			
Lepidopt. larvae	20.6	34.5	16.7	4.8	Indiana/several habitats	Whitaker, 1966	
corn	4.1	4.2	3.2	8.7			
misc. veg.	15.8	3.1	8.0	13.4			
wheat seeds	6.5	1.6	3.2	23.7	(% volume; stomach		
unident. seeds	5.4	5	8.8	8.3	contents)		
green veg.	7.6	0	4.3	3.7	,		
Echinochloa							
seeds	0	1.2	6.4	0			
Coleoptera	3.9	5.3	5.1	1.4			
soybeans	13.4	3.1	6.9	10.7			
Hemiptera	1.3	2.7	4.2	0.9			
beetles	14.6	23.8	9.4	4.9	Colorado/short grass prairie	Flake, 1973	
grasshoppers	6.4	4.2	6.4	2.5			
leafhoppers	13.3	1.8	1.9	2.5	(% volume by a ranking		
Lepidopterans	21.7	12.7	1.5	1.8	method; stomach contents)		
spiders	2.6	2.7	2.5	0.3			
seeds	22.5	25.9	56.8	65.4			
forbs	4.7	10.0	5.6	4.3			
grasses &							
sedges	4.0	2.6	2.8	4.8			
shrubs	3.8	1.4	0.8	2.6			

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location (subspecies)/Habitat	Reference	Note No.
Home Range Size (ha)	A M summer A F summer	0.039 ±0.0054 SD 0.027 ±0.0047 SD		Utah/subalpine meadow snowfree	Cranford, 1984	
	A M winter A F winter	0.019 ±0.0065 SD 0.014 ±0.0050 SD		Utah/subalpine meadow snowbound	Cranford, 1984	
	B M B F	0.058 ± 0.006 SE 0.061 ± 0.005 SE	0.054 - 0.065 0.054 - 0.072	Virginia/mixed deciduous forest	Wolff, 1985a	
	A M A F	0.10 ± 0.0063 SE 0.075 ±0.0063 SE		Oregon/ponderosa pines	Bowers & Smith, 1979	
	A M A F	0.128 ± 0.012 SE 0.094 ±0.0013 SE		Idaho/(<i>artemisiae-sarcobatus</i>) desert	Bowers & Smith, 1979	
Population Density	ВВ	0.19		Arizona/desert	Brown & Zeng, 1989	
(N/ha)	A B summer	2.8		Colorado/subalpine meadows	Vaughn, 1974	
	B B summer B B winter		12.8 - 22.4 3.4 - 8.4	Utah/subalpine meadow	Cranford, 1984	
	АВ		12.7 - 45.5	British Columbia, Canada/burnt	Sullivan, 1979	
	ВВ	12 ± 6.7 SD	3.9 - 28	slash Montana/understory near river	Metzgar, 1979	
Litter		3.4		Virginia (<i>nubiterrae</i>)/NS	Wolff, 1985b	
Size		4.4 5.1 ± 0.14 SE	3.0 - 6.4 1 - 8	average for North America/NS Alberta, Canada (nebrascensis)/NS	Millar, 1989 Millar, 1985	
Litters/Year		2.4 1.9 ± 0.1 SE		average for North America/NS Alberta, Canada (<i>borealis</i>)/various alpine	Millar, 1989 Millar & Innes, 1983	

Population Dynamics	Age/Sex/		B	1 (() () () () () () () () () () (hitet Defenses	Note
Dynamics	Cond./Seas.	Mean	Range	Location (subspecies)/Ha	ıbitat Reference	No.
Days Gestation	F non-lact. F lactating	23.6 26.9		average for United States	/NS Millar, 1989	
	F non-lact. F lactating	22.4 ± 0.1 SE 24.1 ± 0.3 SE	22 - 23 22 - 27	Kansas/NS	Svendsen, 1964	16
	F non-lact. F lactating	25.5 ± 0.3 SE 29.5 ± 1.4 SE	23 - 26 24 - 35	Alberta, Canada (nebrascensis)/lab	Millar, 1985	
Age at Weaning (days)	B B	20.2 24.9 17.5	16 - 25	average for North America Alberta, Canada (borealis)/various alpine Colorado/NS	Millar & Innes, 1983	16
Age at Sexual Maturity	M F	35 days 60 days		Alberta, Canada (nebrascensis)/lab	Millar, 1985	
Mortality Rates	A F winter A M winter J F winter J M winter	100%/winter 33%/winter 56%/winter 70%/winter		Alberta, Canada (borealis various alpine	Millar & Innes, 1983	
	A B summer J B summer	20%/2 weeks 19%/2 weeks		Alberta, Canada (<i>borealis</i> various alpine	Millar & Innes, 1983	
Longevity	ВВ	< 1 yr		Alberta, Canada (borealis various alpine	Miller & Innes, 1983	
Seasonal Activity	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Mating	April November March May		August April October August	Massachusetts Texas Virginia (<i>nubiterrae</i>) California	Drickamer, 1978 Blair, 1958 Wolff, 1985b Dunmire, 1960	16 16 16 16
Dispersal		spring (males)		Vancouver, Canada	Fairbairn, 1977	

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Deer Mouse (Peromyscus maniculatus)

Seasonal Activity	Begin	Peak	End	Location (subspecies)	Reference	Note No.
Torpor		winter		northern parts of range	Tannenbaum & Pivorun, 1989	

- 1 Cited in Montgomery (1989).
- 2 Growth rate of "newly emerged" pups, soon after leaving the nest.
- 3 Temperatures during winter averaged -17.7 °C (-6 to -22 °C); during spring averaged 14.5 °C (8 to 22 °C); during summer 20.6 °C (14 to 32 °C).
- 4 Estimated by authors from laboratory-derived model assuming no reproduction, molt, or weight change and assuming summer temperatures averaged 17.5°C above ground and 20.2°C in burrows and winter temperatures averaged -3°C above ground and 10.7°C in burrows.
- 5 Estimated using equation 3-48 (Nagy, 1987) and body weights from Millar (1989).
- 6 Diet of rat chow with 3 percent water content and 4.5 kcal/g dry weight.
- 7 Diet of Purina lab chow no. 5001; composition not specified.
- 8 Diet of lab chow; composition not specified.
- 9 Diet of lab chow with 8 to 10 percent water content.
- 10 Mean varied by subspecies; sonoriensis, eremicus, gambelii, and fraterculus tested. Dry diet prepared in lab, probably less than 10 percent water content; air temperature 21 to 24°C.
- 11 Dry air at 32 to 34°C; diet of wheat and peanuts, about 10 percent water content.
- 12 Temperature 20 °C ± 2 °C; diet of lab chow with 8 to 10 percent water content.
- 13 Estimated using equation 3-17 (Calder and Braun, 1983) and body weights from Millar (1989).
- 14 Estimated using equation 3-20 (Stahl, 1967) and body weights from Millar (1989).
- 15 Estimated using equation 3-22 (Stahl, 1967) and body weights from Millar (1989).
- 16 Cited in Millar (1989).

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2.2.8. Prairie Vole (voles)

Order Rodentia Family Muridae (subfamily Arvicolinae). New world voles are small, herbivorous rodents that reside in all areas of the United States where good grass cover exists. Their presence is characterized by narrow runways through matted grasses. Microtus species are adapted to underground, terrestrial, and sometimes semiamphibious habitats (Johnson and Johnson, 1982). They are active by day and night and feed mainly on shoots, grasses, and bark (Johnson and Johnson, 1982). Voles are prey for snakes, raptors, and mammalian predators such as short-tailed shrews, badgers, raccoons, coyotes, and foxes (Eadie, 1952; Johnson and Johnson, 1982; Martin, 1956).

Selected species

The prairie vole (*Microtus ochrogaster*) represents the ground-burrowing members of this group. This vole is found in the north and central plains of the United States and in southern Canada, usually in dry places such as prairies and along fencerows and railroads. Its range has expanded eastward to West Virginia as a result of clear-cutting of forests (Jones et al., 1983). Voles are active by day or night (Johnson and Johnson, 1982). Although prairie and meadow voles usually occupy different habitats, where they coexist their population densities tend to be negatively correlated (Klatt, 1985; Krebs, 1977).

Body size. The prairie vole measures from 8.9 to 13 cm in length and has a 3.0- to 4.1-cm tail (Burt and Grossenheider, 1980). After reaching sexual maturity, voles continue to grow for several months (Johnson and Johnson, 1982). Adults weigh from 30 to 45 g (see table). Prairie voles maintain a relatively constant proportion of their body weight as fat (15 to 16 percent on a dry-weight basis) throughout the year (Fleharty et al., 1973).

Habitat. The prairie vole inhabits a wide variety of prairie plant communities and moisture regimes, including riparian, short-grass, or tall-grass communities (Kaufman and Fleharty, 1974). Prairie voles prefer areas of dense vegetation, such as grass, alfalfa, or clover (Carroll and Getz, 1976); their presence in a habitat depends on suitable cover for runways (Kaufman and Fleharty, 1974). They will tolerate sparser plant cover than the meadow vole because the prairie vole usually nests in burrows at least 50 mm underground or in grass nests under logs or boards (Klatt and Getz, 1987).

Food Habits. Meadow voles, as other voles, are largely herbivorous, consuming primarily green succulent vegetation but also roots, bark, seeds, fungi, arthropods, and animal matter (Johnson and Johnson, 1982; Lomolino, 1984; Stalling, 1990). Voles have masticatory and digestive systems that allow them to digest fibrous grasses such as cereals (Johnson and Johnson, 1982). Diet varies by season and habitat according to plant availability, although meadow and other voles show a preference for young, tender vegetation (Johnson and Johnson, 1982; Martin, 1956). Voles can damage pastures, grasslands, crops such as hay and grain, and fruit trees (by eating bark and roots) (Johnson and Johnson, 1982).

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Temperature regulation and molt. Unlike some other mammals, prairie voles do not hibernate or exhibit torpor (Johnson and Johnson, 1982). They overwinter without using their lipid reserves, finding food to meet their metabolic requirements year-round (Fleharty et al., 1973). Prairie voles use burrows, runways, nests, and snow cover to help maintain their body temperature. They also modify when they are active to avoid excessively hot or cold temperatures (Johnson and Johnson, 1982). Voles undergo three molts (juvenile, subadult, and adult), and molting may occur at any time during the year (Jameson, 1947, as cited in Stalling, 1990). The subadult-to-adult molt occurs between 8 and 12 weeks of age (Martin, 1956).

Breeding activities and social organization. Prairie voles are monogamous; a mated pair occupies the same home range (Thomas and Birney, 1979). Reproduction occurs throughout the year, and gestation lasts approximately 3 wk (Martin, 1956; Keller, 1985; Nadeau, 1985). Both sexes care for the young; paternal activities include runway construction, food caching, grooming, retrieving, and brooding the young (Thomas and Birney, 1979). The young are weaned by about 3 weeks of age (Thomas and Birney, 1979). Reproductive activity peaks from May to October, coinciding with high moisture availability (Martin, 1956; Keller, 1985). Monogamous family units apparently defend territories against other family groups (Ostfeld et al., 1988; Johnson and Johnson, 1982; Thomas and Birney, 1979).

Home range and resources. Prairie voles excavate underground nests that are used as nurseries, resting areas, and as shelter from severe weather (Klatt and Getz, 1987). They spend very little time away from this nest (Barbour, 1963). In thick vegetation, prairie voles move about in surface runways, and the number of runways is proportional to population density (Carroll and Getz, 1976). Female home range size decreases with increasing prairie vole density according to the following regression equation (Gaines and Johnson, 1982):

Y= -0.23X + 20.16 where Y= home range length in meters and X= minimum number alive per 0.8 ha grid.

Abramsky and Tracy (1980) found a similar correlation using both sexes according to the equation:

Y= -0.20X + 27.12 where Y= home range length in meters and X=number of individuals per hectare.

Population dynamics. Female prairie voles can reach sexual maturity in about 35 d, males in 42 to 45 d (Gier and Cooksey, 1967, as cited in Stalling, 1990). Martin (1956) found in Kansas that females mature within about 6 wk in the summer, but may require 15 wk or more to mature if born in the fall. Male prairie voles tend to disperse from their natal site; approximately twice as many females as males mature near their birthplace (Boonstra et al., 1987). Populations tend to fluctuate with available moisture (Gier, 1967, as cited in Stalling, 1990). Mortality rates in prairie vole postnestling juveniles and young adults are similar and higher than adult mortality rates; nestlings have the lowest mortality rate (Golley, 1961). Average life expectancy in the field is about 1 yr (Martin, 1956).

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Similar species (from general references)

- The pine vole (*Microtus pinetorum*) (7 to 11 cm), despite its name, usually inhabits deciduous forest floors, among a thick layer of duff, where it tunnels through loose soil near the surface. It is found in the eastern half of the United States, except Florida; in the south, it inhabits pine forests. In addition to feeding on bark, it burrows for bulbs, tubers, and corms.
- See also similar species listed for the meadow vole in this chapter.

General references

Burt and Grossenheider (1980); Johnson and Johnson (1982); Stalling (1990); Tamarin (1985).

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Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
Body Weight (g)	АВ	41.6		ne Colorado	Abramsky & Tracy, 1980	
	A B summer A B fall A B winter A B spring	41.9 44.2 39.0 41.3		ne Colorado	Abramsky & Tracy, 1980	
	A M A F	31.3 ± 0.35 SE 33.3 ± 0.30 SE		s Indiana	Myers & Krebs, 1971	
	neonate B	2.8 ± 0.4 SD		ne Kansas	Martin, 1956	
Metabolic Rate (IO ₂ /kg-d)	A winter	51.8 ± 8.2 SD		NS/lab	Wunder et al., 1977	
	A summer	41.8 ± 4.8 SD				
Metabolic Rate (kcal/kg-d)	A B basal	177			estimated	1
	A B free-living	399	(190 - 833)		estimated	2
Food Ingestion Rate (g/g-d)	A B at 21°C A B at 28°C	0.13 - 0.14 0.09 - 0.10		Illinois/lab	Dice, 1922	3
Water Ingestion Rate (g/g-d)	A B	0.37		NS/lab	Chew, 1951	4
	AB	0.29 ± 0.02 SE		Kansas/lab	Dupre, 1983	5
	A B	0.21	0.15 to 0.26	Illinois/lab	Dice, 1922	6
	AB	0.14			estimated	7
Inhalation Rate (m³/d)	АВ	0.043			estimated	8
Surface Area (cm²)	АВ	139			estimated	9

Prairie Vole (*Microtus ochrogaster*)

Dietary Composition		Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
Sporobolus asp	er		19.5			Kansas/forb and grass field	Fleharty & Olson, 1969	
Kochia scoparia			22.5			Transactions and grace nota	l ionarty a ciccii, rece	
Bouteloua graci			6.5			(% volume; stomach		
Bromus japonic	us		8.5			contents)		
Rumex crispus			9.2			,		
Triticum aestivum		3.4			(Items less than 2% of			
Carex sp.			2.0			volume were combined as		
other			28.3			"other")		
(grasses)			(53.5)					
(forbs)			(46.5)					
Festuca arundir	nacea	20.5	25.0	10.6	28.9	Missouri/old field	Cook et al., 1982	
Dactylis glomerata 6.7		6.7	1.7	1.1	4.2		,	
Phleum pratense 8.3		2.0	2.1	5.3	(mean number of food			
Tridens flavus 17.1		11.1	1.9	11.0	items; stomach contents)			
Setaria viridis 6.7		6.7	6.2	1.7	6.2	,		
Taraxacum officinale 5.8		5.8	4.8	3.9	1.5	(Plant parts consumed: leaf,		
Lamium amplexicaule 3.9		3.9	2.9	5.2	3.4	stem, and seeds of Festuca		
Bromus tectorum 2.8		2.8	4.7	2.5	4.8	and Bromus; leaf and stem		
Capsella bursa-past. 5.6		5.6	3.9	0.7	21.0	of Tridens and Setaria		
Trifolium stolon		2.7	1.2	0.5	0.6	faberi; leaf and seeds of		
arthropods		2.4	0.8	0.5	1.4	Dactylis and Seteria viridis;		
animal material		0.2	0.3	0.0	0.1	and leaves only of all other		
other		0	0.2	0.2	0.0	plant species)		
		3.9	1.4	1.5	0.9			
Population	Age/S	Sex/						Note
Dynamics	Cond	./Seas.	Mean		Range	Location/Habitat	Reference	No.
Home A B all y		ll yr	0.098 ± 0.012	SE		Illinois/bluegrass	Jike et al., 1988	
Size (ha)	A M a	<u>-</u>			Kansas/NS	Swihart & Slade, 1989		
	A M A F		0.011 0.0073			ne Colorado/short-grass	Abramsky & Tracy, 1980	

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Population Density (N/ha)	summer winter	25 - 35 12		w Nebraska/xeric prairie	Meserve, 1971	
	spring summer	78 - 118 81 - 104		Illinois/alfalfa field	Carroll & Getz, 1976	
	summer winter spring fall	168 - 234 160 - 197 203 - 247 94 - 123		ne Kansas/grassland	Martin, 1956	
Litter Size		3.18 ± 0.24 SD 3.4 4.25	1 - 7	ne Kansas/grassland Kansas/NS Illinois/NS	Martin, 1956 Jameson, 1947 Cole & Batzli, 1978	10 11 12
Litters/Year		several		NS/NS	Johnson & Johnson, 1982	
Days Gestation		21 21		ne Kansas/grassland NS/NS	Martin, 1956 Keller, 1985	
Pup Growth Rate (g/d)	days 1 to 10 days 11 to 30 > 30 d until growth stops	0.6 1.0 0.5 (highly variable)		ne Kansas/grassland	Martin, 1956	
Age at Weaning		21 days		NS/lab	Thomas & Birney, 1979	
Age at Sexual Maturity	F M	35 days	42 to 45 d	NS/NS	Gier & Cooksey, 1967	13
Annual Mortality	В	93 %		ne Colorado/short-grass prairie	Abramsky & Tracy, 1980	
Longevity	В	1 yr	up to 1.8 yr	ne Kansas/grassland	Martin, 1956	

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Prairie Vole (Microtus ochrogaster)

Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating		May to Oct		NS	Keller, 1985; Martin, 1956	
Parturition		May to Oct		NS	Keller, 1985; Martin, 1956	
Molt		any time		NS	Jameson, 1947	13

- 1 Estimated using equation 3-43 (Boddington, 1978) and body weights (summer) from Abramsky and Tracy (1980).
- 2 Estimated using equation 3-48 (Nagy, 1987) and body weights (summer) from Abramsky and Tracy (1980).
- 3 Estimated from ingestion rate for diet of oats (74 to 78 percent of total weight of diet) and dry grass, assuming 31 to 34 g body weight. Diet was low in water (probably less than 10 percent).
- 4 Measured water drunk from water bottles; diet consisted of rolled oats with sunflower seeds; temperature 28°C.
- 5 Measured water drunk; diet of dry food.
- 6 Temperature 21°C; dry air.
- 7 Estimated using equation 3-17 (Calder and Braun, 1983) and body weights (summer) from Abramsky and Tracy (1980).
- 8 Estimated using equation 3-20 (Stahl, 1967) and body weights (summer) from Abramsky and Tracy (1980).
- 9 Estimated using equation 3-22 (Stahl, 1967) and body weights (summer) from Abramsky and Tracy (1980).
- 10 Determined from pup count, which may underestimate litter size at birth.
- 11 Cited in Keller (1985); embryo or pup count.
- 12 Cited in Keller (1985); embryo or placental scar count.
- 13 Cited in Stalling (1990).

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2.2.9. Meadow Vole (voles)

Order Rodentia Family Muridae (subfamily Arvicolinae). New world voles are small, herbivorous rodents that reside in all areas of Canada and the United States where there is good grass cover. Their presence is characterized by narrow runways through matted grasses. Microtus species are adapted to underground, terrestrial, and sometimes semiamphibious habitats (Johnson and Johnson, 1982). They are active by day and night, feeding mainly on shoots, grasses, and bark. Voles are prey for hawks and owls as well as several mammalian predators such as short-tailed shrews, badgers, and foxes (Johnson and Johnson, 1982; Eadie, 1952).

Selected species

The meadow vole (*Microtus pennsylvanicus*) makes its burrows along surface runways in grasses or other herbaceous vegetation. It is the most widely distributed small grazing herbivore in North America and is found over most of the northern half of the United States. Meadow voles have been used in bioassays to indicate the presence of toxins in their foods (Kendall and Sherwood, 1975, cited in Reich, 1981; Schillinger and Elliot, 1966). Although primarily terrestrial, the meadow vole also is a strong swimmer (Johnson and Johnson, 1982).

Body size. The meadow vole measures 8.9 to 13 cm in length (head and body) and has a 3.6- to 6.6-cm tail. They weigh between 20 and 40 g depending on age, sex, and location (see table). Mature males are approximately 20 percent heavier than females (Boonstra and Rodd, 1983). Meadow voles lose weight during the winter, reaching a low around February, then regain weight during spring and summer, reaching a high around August in many populations (see table; Iverson and Turner, 1974).

Habitat. The meadow vole inhabits grassy fields, marshes, and bogs (Getz, 1961a). Compared with the prairie vole, the meadow vole prefers fields with more grass, more cover, and fewer woody plants (Getz, 1985; Zimmerman, 1965). The meadow vole also tends to inhabit moist to wet habitats, whereas the prairie vole is relatively uncommon in sites with standing water (Getz, 1985).

Food habits. Meadow voles consume green succulent vegetation, sedges, seeds, roots, bark, fungi, insects, and animal matter (see table). They are agricultural pests in some areas, feeding on pasture, hay, and grain (Johnson and Johnson, 1982; Burt and Grossenheider, 1980). At high population densities, the meadow vole has been known to girdle trees, which can damage orchards (Byers, 1979, cited in Reich, 1981). In seasonal habitats, meadow voles favor green vegetation when it is available and consume other foods more when green vegetation is less available (Johnson and Johnson, 1982; Riewe, 1973; Getz, 1985). Although Zimmerman (1965) found some evidence of food selection, he found that meadow voles generally ate the most common plants in their habitat. Meadow voles living on prairies consume more seeds and fewer dicots and monocots than voles in a bluegrass habitat (Lindroth and Batzli, 1984). The meadow vole's large cecum allows it to have a high digestive efficiency of 86 to 90 percent (Golley, 1960). Coprophagy (eating of feces) has been observed in this species (Ouellete and Heisinger, 1980).

Temperature regulation and molt. In winter, Microtus species do not undergo hibernation or torpor; instead, they are active year round (Didow and Hayward, 1969; Johnson and Johnson, 1982). Behaviors that help meadow voles to maintain their body temperature include the use of burrows, runways, nests, and snow cover for insulation. They also can change when they are active; when temperatures exceed 20°C, meadow voles are most active at night (Getz, 1961b; Johnson and Johnson, 1982). In winter, meadow voles increase their brown fat content (a major site of thermoregulatory heat production). Mature individuals average 0.5 percent brown fat in summer, increasing to 1.7 percent in early winter; juveniles average 1.0 percent in the summer, increasing to 2.3 percent in the winter (Didow and Hayward, 1969). Voles undergo three molts: juvenile, postjuvenile, and adult. The timing varies by species (Johnson and Johnson, 1982). Adult Arvicolinae also undergo winter and summer molts (Johnson and Johnson, 1982).

Breeding activities and social organization. Meadow voles are polygynous (McShea, 1989). Males form a hierarchy in which the most dominant male voles breed (Boonstra and Rodd, 1983). Voles produce litters throughout the breeding season, the number of litters per season increases with decreasing latitude (Johnson and Johnson, 1982).

Home range and resources. The area encompassed by a meadow vole's home range depends on season, habitat, population density, and the age and sex of the animal. Summer ranges tend to be larger than winter ranges, and ranges in marshes tend to be larger than ranges in meadows (Getz, 1961c; Reich, 1981). Home range size also declines with increasing population density (Getz, 1961c; Tamarin, 1977a). Female meadow voles defend territories against other females, whereas male home ranges are larger and overlap with home ranges of both sexes (Madison, 1980; Ostfeld et al., 1988; Wolff, 1985). Meadow voles build runways in grasses and vegetation at the ground's surface and use the runways for foraging about 45 percent of the time, depending on weather and other factors (Gauthier and Bider, 1987). The meadow vole exhibits daytime activity where dense cover is available and becomes more crepuscular with less cover (Graham, 1968, cited in Reich, 1981). All *Microtus* species apparently do some burrowing, excavating underground nests that are used as nurseries, resting areas, and as shelter from severe weather (Johnson and Johnson, 1982). Nests are built with the use of dead grass in patches of dense, live grass; widened spaces, called forms, are used off main runways (Ambrose, 1973).

Population density. Meadow vole population densities fluctuate widely from season to season and year to year, sometimes crashing to near zero before recovering in a few years to densities of several hundred per hectare (Boonstra and Rodd, 1983; Lindroth and Batzli, 1984; Getz et al., 1987; Myers and Krebs, 1971; Taitt and Krebs, 1985). Krebs and Myers (1974) noted population cycles of 2 to 5 yr, whereas Tamarin (1977b) reported 3- to 4-year population cycles in southeastern Massachusetts. However, Getz et al. (1987) found no indication of multiannual abundance cycles in their three habitat study (i.e., bluegrass, tallgrass prairie, and alfalfa) in east central Illinois. Meadow voles avoid short-tailed shrews (Fulk, 1972), and the vole population density decreases as the number of short-tailed shrews in the area increases (Eadie, 1952).

Population dynamics. Voles reach sexual maturity usually within several weeks after birth, with females maturing before males, but still continue to grow for several months (Johnson and Johnson, 1982). Innes (1978) reported that litter size is independent of latitude or elevation. However, summer litters were, on average, 14 percent larger than litters produced during other seasons, and larger females produced larger litters (Keller and Krebs, 1970). Young from the spring and early summer litters reached adult weight in about 12 wk (Brown, 1973). Mortality rates are highest in postnestling juveniles and young adults and lowest in nestlings (ages 1 to 10 d) (Golley, 1961). Dispersing meadow voles (predominantly young males) tend to weigh less than resident meadow voles (Boonstra et al., 1987; Myers and Krebs, 1971; Boonstra and Rodd, 1983; Brochu et al., 1988).

Similar species (from general references)

- The California vole (*Microtus californicus*) is larger than the meadow vole (12 to 14 cm head and body) and is found throughout California and southern Oregon. It inhabits freshwater and saltwater marshy areas, wet meadows, and grassy hillsides from the seashore to the mountains and feeds on green vegetation.
- Townsend's vole (*Microtus townsendii*) usually is found near water in moist fields, sedges, tules, and meadows (from tidewater to alpine meadows). Its range is limited to extreme northwestern California, western Oregon and Washington, and southern British Columbia (inhabits several islands off the coast of Washington and British Columbia). It is easily distinguished by its large size (12 to 16 cm) and black-brown color.
- The montane vole (*Microtus montanus*) (mountain vole) is slightly larger (10 to 14 cm) than the meadow vole and is found in valleys of the mountainous Great Basin area of the western and northwestern United States.
- The long-tailed vole (Microtus longicaudus) (tail 5 to 9 cm) is slightly larger (11 to 14 cm) than the meadow vole. It is found in the western United States and Canada to Alaska and lives along streambanks, in mountain meadows, sometimes in dry situations, and in brushy areas during winter. In addition to grasses and bark, it feeds on bulbs. It nests above ground in winter and burrows in summer.
- The creeping vole (*Microtus oregoni*) (Oregon vole) (10 to 11 cm) is an inhabitant of western Oregon and Washington and extreme northwest California. Seldom above ground, it spends most of its time burrowing through forest floor duff or grass roots. It lives in forests, brush, and grassy areas.
- The sagebrush vole (*Lagurus curtatus*) (9.7 to 11 cm) lives in loose soil and arid conditions and feeds on green vegetation, especially sagebrush. It also burrows around sagebrush; a vole found living in sagebrush is almost certainly this species.

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Meadow Vole

General references

Burt and Grossenheider (1980); Reich (1981); Johnson and Johnson (1982); Tamarin (1985).

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location	Reference	Note No.
A F avg. all yr	A F summer A M spring A F spring A M & F spring summer fall winter A M avg. all yr	40.0 ± 8.3 SE 33.4 ± 8.2 SE 52.4 43.5 26.0 24.3 17.0 17.5 35.5 ± 0.1 SE 39.0 ± 0.3 SE		Quebec, Canada Ontario, Canada Manitoba, Canada south Indiana	Brochu et al., 1988 Boonstra & Rodd, 1983 Anderson et al., 1984 Myers & Krebs, 1971	
	neonate M & F neonate M & F	2.1 2.3 ± 0.1 SD	1.6 - 3.0	not specified	Hamilton, 1941 Innes & Millar, 1981	1 2
Pup Growth Rate (g/d)	birth - 21 days 22 - 33 days 34 - 54 days 55 - 103 days	0.95 0.81 0.45 0.19		south Michigan/old field	Golley, 1961	
Body Fat (g)	summer: J F A F gestating A F lactating	0.37 ± 0.04 SE 1.20 ± 0.15 SE 0.60 ± 0.09 SE		Alberta, Canada	Millar, 1987	
Metabolic Rate (IO ₂ /kg-d)	basal average daily	60.0 82.8 ± 12 SD	43.2 - 146	lab lab	Wiegert, 1961 Morrison, 1948	3 4
Metabolic Rate (kcal/kg-d)	A M basal A F basal A B avg. daily A M free-living A F free-living	166 175 395 357 485	(170 - 747) (231 - 1,020)	lab 25-30°C	estimated Pearson, 1947 estimated	5 6

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Factors	Age/Sex/ Cond./Seas	. Mean		Range or (95% CI of mean)	Location	Reference	Note No.
Food Ingestion Rate (g/g-d)		0.30 - 0.	35		Russia	Ognev, 1950	7
(cal/g-d)	A M short-d A M long-da				NS	Dark et al., 1983	8
Water	АВ	0.21 ± 0	.02 SE		NS	Ernst, 1968	9
Ingestion Rate (g/g-d)	AB	0.14				estimated	10
Inhalation Rate (m³/d)	A M A F	0.052 0.044				estimated	11
Surface Area (cm²)	A M A F	161 143				estimated	12
Dietary Composition	Spring	Summer	Fall	Winter	Location/Habitat (measure)	Reference	Not No.
dicot shoots monocot shoots	41 50	60 26	66 9	12 40	Illinois/bluegrass	Lindroth & Batzli, 1984	
seeds	1	9	1	13	(% volume; stomach		
roots	0	1	12	34	contents)		
fungi insects	6 2	4 0	10 2	0			
dicot shoots	53	65	41	41	Illinois/tallgrass prairie	Lindroth & Batzli, 1984	
monocot	23	29	12	5	minois/tanglass plante	Zilidiotii & Datzii, 1904	
shoots					(% volume; stomach		
seeds	7	1	16	36	contents)		
roots	4	0	6	17			
fungi	12	1 1	20	0			
insects	∣ 1	4	5	⊢ 1			I

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Home Range Size (ha)	A M summer A F summer	0.019 ± 0.011 SD 0.0069 ±0.0039 SD		Virginia/old field	Madison, 1980	
	A B summer A B winter	0.014 0.0002		Montana/alluvial bench	Douglass, 1976	
	A M summer A F summer	0.083 ± 0.037 SD 0.037 ± 0.020 SD		Massachusetts/grassy meadow	Ostfeld et al., 1988	
Population Density (N/ha) A B A B A B fall winter spring summer	AB		96 - 549 2 - 28 25 - 163	Ontario, Canada/grassland Illinois/bluegrass Indiana/grassland	Boonstra & Rodd, 1983 Lindroth & Batzli, 1984 Myers & Krebs, 1971	
	winter spring		28 - 51 20 - 51 22 - 53 38 - 64	Michigan/grass-sedge marsh	Getz, 1961a	
Litter Size		3.82 4.46 6.05	1 - 11 1 - 9 1 - 8	Manitoba, Canada/NS Indiana/NS Pennsylvania/NS	Iverson & Turner, 1976 Corthum, 1967 Goin, 1943	13 13 13
Litters/Year		several		NS/NS	Bailey, 1924	14
Days Gestation		21.0 ± 0.2 SD		NS/NS	Kenney et al., 1977	2
Age at Weaning (d)		21		s Michigan/NS	Golley, 1961	
Age at Sexual Maturity	F M		at least 3 wk at least 6-8 wk	NS/NS	Johnson & Johnson, 1982	
Mortality Rates	nestlings juveniles young adults adults old adults	(0-10 g) 50% (11-20 g) 61% (21-30 g) 58% (31-50 g) 53% (>50 g) 100%		south Michigan/old field	Golley, 1961	

Meadow Vole (Microtus pennsylvanicus)

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Longevity		2-3 mo	< 24 mo	NS NS	Beer & MacLeod, 1961 Johnson & Johnson, 1982	9
Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	early April	Oct Nov. April - June	mid-October	Manitoba, Canada Michigan (fall-winter peak) Michigan (spring-summer peak)	Mihok, 1984 Getz, 1960 Getz, 1960	15 15
Dispersal		fall/winter		Indiana/grassland	Myers & Krebs, 1971	
		summer (females) winter (males)		Massachusetts/coastal field	Tamarin, 1977b	

- 1 Cited in Reich (1981) and Johnson and Johnson (1982).
- 2 Cited in Nadeau (1985).
- 3 Body weight 35.6 g; temperature not specified; cited in Deavers and Hudson (1981).
- 4 Temperature 15 to 25 °C; weight 26.2 to 32 g.
- 5 Estimated using equation 3-43 (Boddington, 1978) and body weights from Anderson et al. (1984).
- 6 Estimated using equation 3-48 (Nagy, 1987) and body weights from Anderson et al. (1984).
- 7 Cited in Johnson and Johnson (1982).
- 8 Short-day photoperiod = 10 h of light, 14 of dark; long-day photoperiod = 14 h of light, 10 of dark.
- 9 Cited in Reich (1981).
- 10 Estimated using equations 3-17 (Calder and Braun, 1983) and 3-18 and body weights from Anderson et al. (1984).
- 11 Estimated using equation 3-20 (Stahl, 1967) and body weights from Anderson et al. (1984).
- 12 Estimated using equation 3-22 (Stahl, 1967) and body weights from Anderson et al. (1984).
- 13 Cited in Keller (1985).
- 14 Cited in Johnson and Johnson (1982).
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2.2.10. Muskrat (water rats and muskrats)

Order Rodentia Family Muridae. Water rats and muskrats are the most aquatic of this family of rodents, with most of their lives spent in or near bogs, marshes, lakes or streams. These two rodents feed mostly on aquatic vegetation. Only one species exists in each genus (Burt and Grossenheider, 1980).

Selected species

The muskrat (*Ondatra zibethicus*) is indigenous and common throughout most of the United States (except in the extreme southeast, central Texas, and most of California) and Canada (except in the extreme north) (Burt and Grossenheider, 1980). Muskrats feed primarily on aquatic plants. They are prey for hawks, minks, otters, raccoons, owls, red fox, dogs, snapping turtles, and water snakes (Bednarik, 1956; Errington, 1939a; Wilson, 1985), and are more vulnerable to predation during times of drought when low water levels leave their dens or lodges more exposed (Errington, 1939a). Many vertebrates use muskrat homes for shelter or to find food (Kiviat, 1978). The muskrat is one of the most valuable fur animals in North America (Dozier, 1953; Perry, 1982). Including the Newfoundland muskrat, formerly *Ondatra obscurus*, 16 recognized subspecies of *O. zibethicus* exist in North America (Perry, 1982). Of these, *O. z. zibethicus* (eastern United States, southeastern Canada), *O. z. osoyoosensis* (Rocky Mountains, southwestern Canada), and *O. z. rivalicius* (southern Louisiana, coasts of Mississippi, western Alabama, and eastern Texas) are most often studied.

Body size. The muskrat measures 25 to 36 cm (head and body) with a 20- to 25- cm tail (Burt and Grossenheider, 1980), and adult weights can range from 0.5 kg to over 2 kg (see Appendix). Willner et al. (1980) reported no sexual dimorphism, whereas Dozier (1950), Parker and Maxwell (1984), and others (see Appendix) reported that males are slightly heavier than females. Muskrats tend to be larger and heavier in northern latitudes (Perry, 1982), although the smallest muskrats are found in Idaho (Reeves and Williams, 1956). Fat levels in adult males increase from spring through fall, and subsequently decrease from winter to spring (Schacher and Pelton, 1975). In nonpregnant females, fat levels decrease from winter through summer; in pregnant females, body fat increases from spring to summer (Schacher and Pelton, 1975).

Habitat. Muskrats inhabit saltwater and brackish marshes and freshwater creeks, streams, lakes, marshes, and ponds (Dozier, 1953; Johnson, 1925; Kiviat, 1978; O'Neil, 1949). Muskrats that live along the banks or shores of waterways generally excavate dens in the banks, whereas muskrats living in ponds with ample plant material construct lodges (Johnson, 1925; Perry, 1982). When available, bank dens seem preferred over constructed lodges (Johnson, 1925).

Food habits. Muskrats are primarily herbivorous, but some populations are more omnivorous (Dozier, 1953; Errington, 1939b). Muskrats usually feed at night, diving to gnaw on aquatic vegetation growing near their houses (Dozier, 1953; Johnson, 1925; Perry, 1982). The roots and basal portions of aquatic plants make up most of the muskrat's diet, although shoots, bulbs, tubers, stems, and leaves also are eaten (Dozier,

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1950, 1953; Willner et al., 1980; Svihla and Svihla, 1931). Marsh grasses and sedges (Svihla and Svihla, 1931) and cattails (Johnson, 1925; Willner et al., 1975) seem to be important muskrat foods; in Maryland, green algae is also important (Willner et al., 1975). Although muskrats forage near their dens or lodges, they show preferences for some plant species (e.g., cattails, bulrushes) over others (Bellrose, 1950). Muskrats are a major consumer of marsh grasses (Kiviat, 1978). They also dig for food on lake and pond bottoms (Bailey, 1937; Dozier, 1953; Hanson et al., 1989). Among the animals that muskrats consume are crayfish, fish, frogs, turtles, and young birds (Errington, 1939b; Johnson, 1925; Willner et al., 1980). Molluscs are an important component of the diet of some populations (Convey et al., 1989; Neves and Odom, 1989; Parmalee, 1989; Willner et al., 1980). Young muskrats feed more on bank vegetation than do adults (Warwick, 1940, cited in Perry, 1982).

Temperature regulation and molt. Active year-round (Kiviat, 1978), muskrats usually begin their annual molt in the summer, with fur reaching its minimum density during August (Willner et al., 1980). Muskrats use their dens or lodges to insulate themselves from summer heat and winter cold (O'Neil, 1949; Willner et al., 1980). During extreme cold, muskrats may freeze to death if they are unable to plug their den entrances (Errington, 1939a).

Breeding activities and social organization. Muskrats are solitary or form breeding pairs that remain in a home range exclusive of other pairs (Errington, 1963; Proulx and Gilbert, 1983). They are territorial, particularly during peak reproductive activity, with their houses usually spaced at least 8 m apart (Johnson, 1925; Sather, 1958; Trippensee, 1953). In southern parts of their range, muskrats breed throughout the year, with late fall and early spring peaks (O'Neil, 1949; Svihla and Svihla, 1931; Wilson, 1955). In northern latitudes, breeding occurs only in the spring and summer, with first litters born in late April or early May (Mathiak, 1966; Beer, 1950; Errington, 1937b; Gashwiler, 1950). Errington (1937b) found that postpartum estrus occurs in the muskrat, and suggested that the period between litters is about 30 d. Neonates are almost hairless but by age 2 wk are covered with fur and able to swim (Errington, 1963).

Home range and resources. Muskrats have relatively small home ranges that vary in configuration depending on the aquatic habitat (Perry, 1982; Willner et al., 1980). They build two different types of houses: a main dwelling and a feeding house (feeder) that is smaller than the main house (Dozier, 1953; Johnson, 1925; Sather, 1958). The feeder provides protection from the elements and predators when feeding in prime foraging areas, as well as access to oxygen during frozen conditions. The house provides a dry nest and stable temperatures. Muskrats usually forage within 5 to 10 m of a house (Willner et al., 1980). Using radiotelemetry, MacArthur (1978) found muskrats within 15 m of their primary dwelling 50 percent of the time and only rarely more than 150 m. Mathiak (1966) reported other experiments showing that muskrats remain close to their dwellings.

In the winter, muskrats build pushups, which are cavities formed in 30 to 46 cm high piles of vegetation pushed up through holes in the ice of a marsh (Perry, 1982). Muskrats use pushups as resting places during frozen conditions to minimize their exposure to cold water (Fuller, 1951). In the summer, muskrats often change the use of their home range in response to water levels; during droughts they will move if the area

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around the house dries up, which can lead to intense aggression in the more favorable habitat (Errington, 1939a). Usually only a minor proportion of drought-evicted muskrats can find new homes (Errington, 1939a). In the winter, droughts can result in severe mortality (Errington, 1937a).

Population density. Bellrose and Brown (1941, cited in Perry, 1982) concluded that cattail communities support more muskrat houses than other plant types in the Illinois River valley. Cattail communities also support high densities of muskrats in other areas (Errington, 1963; Dozier, 1950). In pond and lake habitats, shoreline length is a more important factor than overall habitat area in determining muskrat density (Glass, 1952, cited in Perry, 1982). Many investigators estimate muskrat densities by counting the number of houses or push-ups and multiplying by a factor ranging from 2.8 (Lay, 1945, cited in Boutin and Birkenholz, 1987) to 5.0 (Dozier et al., 1948), although this method is questionable (Boutin and Birkenholz, 1987).

Population dynamics. The age at first breeding varies but usually occurs during the first spring after birth (Errington, 1963; Perry, 1982). Southern populations produce more litters but with fewer pups in each than do northern populations (Boyce, 1977; Perry, 1982; see table). Muskrats in lower quality habitats have both smaller litter sizes and fewer litters than muskrats in better quality areas (Neal, 1968). They disperse in the spring to establish breeding territories or to move into uninhabited areas (Errington, 1963). Muskrat population cycles of 5, 6, and 10 y have been reported (Butler, 1962; Willner et al., 1980); Perry (1982) summarized several studies that reported cycles ranging from 10 to 14 yr or more. Butler (1962) found that muskrats follow a 10-yr cycle in most parts of Canada.

Similar species (from general references)

• The Florida water rat (*Neofiber alleni*) is much smaller (20 to 22 cm) than the muskrat, with a rounded tail (11 to 17 cm) to distinguish it further. The Florida water rat inhabits bogs, marshes, weedy lake borders, and savanna streams, though its range is limited to Florida. It feeds on aquatic plants and crayfish.

General references

Boutin and Birkenholz (1987); Burt and Grossenheider (1980); Perry (1982); Willner et al. (1980).

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Muskrat (Ondatra zibethicus)

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% Cl of mean)	Location	Reference	Note No.
Body Weight (g)	B M winter B F winter	1,480 1,350	1,400 - 1,520 1,300 - 1,400	New York	Dozier, 1950	
	B M winter B F winter	1,326 ± 45.9 SE 1,221 ± 54.2 SE		e Tennessee	Schacher & Pelton, 1978	
	B M winter B F winter	1,180 1,090	730 - 1,550 770 - 1,450	Nebraska, nc Kansas	Sather, 1958	
	A M spring A F spring	909 837		Idaho	Reeves & Williams, 1956	
	neonate neonate	21.3	16 - 28 20 - 25	lowa New York	Errington, 1939b Dean, 1957	
	at weaning at weaning	200	112 - 184	lowa New Brunswick, Canada	Errington, 1939b Parker & Maxwell, 1984	
Pup Growth Rate (g/d)	0 to 30 d weaning to 1st	5.4	4.3 - 5.6	lowa/marsh	Errington, 1939b	
11010 (3,0)	fall; M F	7.5 7.1		New Brunswick, Canada/ marsh	Parker & Maxwell, 1980	
Metabolic Rate (IO ₂ /kg-d)	floating swimming	21 ± 7.9 SE 38		lab (water temperature 25°C)	Fish, 1982	
Metabolic Rate (kcal/kg-d)	floating swimming	101 182		lab (water temperature 25°C)	Fish, 1982	
	A M basal A F basal	71.6			estimated	1
	A M free-living A F free-living	213 216	(90 - 505) (91 - 513)		estimated	2

Factors	Age/Sex/ Cond./Seas.	Mea	1	ange or 5% CI of mean)	Location	Reference	Note No.
Food Ingestion Rate (g/g-d)	greens greens & corr	0.34 0.26			Louisiana, captive (rivalicius)	Svihla & Svihla, 1931	3
Water Ingestion Rate (g/g-d)	A M A F	0.97 0.98				estimated	4
Inhalation Rate (m³/d)	A M A F	0.61 0.57				estimated	5
Surface Area (cm²)	A M A F	1,22 1,15				estimated	6
Dietary Composition	Spring	Summe	Fall	Winter	Location/Habitat (measure)	Reference	Note No.
cattail bulrush burreed waterstarwort pondweed arrowhead corn				25 - 50 10 - 25 5 - 10 2 - 5 2 - 5 2 - 5 2 - 5	ne United States/NS (rough approximation of % diet; stomach contents)	Martin et al., 1951	
cattail rush millet algae grass cord grass seeds other		59 17 8 5 4 4 2			Somerset Co., MD/brackish marsh (% of diet; stomach contents)	Willner et al., 1975	

Dietary Composition	Spring	Summer	Fall		Winter	Location/Habitat (measure)	Reference	Note No.
green algae 3-square rush switch grass soft rush water willow grass (Graminae) other		77 8 8 4 2 1				Montgomery Co., MD/ freshwater (% of diet; stomach contents)	Willner et al., 1975	
Population Dynamics	Age/Sex/ Cond./Seas.	Mean		Rar	nge	Location/Habitat	Reference	Note No.
Home Range Size (ha)	summer early summer late summer	0.17 ± 0.00 0.048 ± 0.03 0.11 ± 0.08	24 SD			Ontario, Canada/marsh Ontario, Canada/bay	Proulx & Gilbert, 1983 Proulx & Gilbert, 1983	
	B M B F	0.17 0.17				lowa/marsh	Neal, 1968	
Population Density	A B spring A B summer A B fall	9.3 ± 1.3 SE 2.6 ± 0.3 SE 6.3 ± 1.1 SE	E/ha			ne lowa/open water riverine	Clay & Clark, 1985	
	B M B M	18.7/ha 2.1/ha				Virginia/fringe marsh Virginia/marsh	Halbrook, 1990	
	ВВ	28.3/ha		1 - 7	74	Louisiana/ <i>Scirpus olneyi</i> marsh	O'Neil, 1949	
	B B summer	23/km river				Pennsylvania/riverine (little vegetation) Massachusetts/wetland,	Brooks & Dodge, 1986 Brooks & Dodge, 1986	
						river (sedges)		
Litter Size		3.46 4.65 7.1 ± 0.2 SE 7.3	Ē	3 - 0		Louisiana/marsh Virginia/marsh lowa/riverine Wisconsin/marsh	O'Neil, 1949 Halbrook, 1990 Clay & Clark, 1985 Mathiak, 1966	

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Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location/Habitat	Reference	Note No.
Litters/Year		1.7 2.1 5 - 6	<7-8	ldaho/marsh Maine/wildlife refuge - NS Louisiana/NS	Reeves & Williams, 1956 Gashwiler, 1950 O'Neil, 1949	
Days Gestation		29 - 30	> 22 - 23	nw Iowa/marsh Maine/wildlife refuge - NS	Errington, 1937b Gashwiler, 1950	
Age at Weaning	В	28 d	21 - 30 d	lowa/marsh	Errington, 1939b	
Age at Sexual Maturity		6 mo		Louisiana/marsh	Svihla & Svihla, 1931	
Annual Mortality Rates (%)	adult juvenile juvenile	87 90 67		ne lowa/riverine Missouri/NS	Clay & Clark, 1985 Schwartz & Schwartz, 1959	7
Longevity			< 5 yr	Ontario, Canada/marsh	Proulx & Gilbert, 1983	
Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	year-round	winter spring-summer		southern latitudes	O'Neil, 1949; Svihla & Svihla, 1931 Chamberlain, 1951; Gashwiler, 1950; Reeves & Williams, 1956	
Parturition	late April early May late May	June early July	late August late August mid-August	lowa Maine Idaho	Errington, 1937b Gashwiler, 1950 Reeves & Williams, 1956	
Dispersal		fall spring		Ontario, Canada Iowa	McDonnell & Gilbert, 1981 Errington, 1963	

Muskrat (Ondatra zibethicus)

- 1 Estimated using equation 3-43 (Boddington, 1978) and body weights from Sather (1958).
- 2 Estimated using equation 3-46 (Nagy, 1987) and body weights from Sather (1958).
- 3 Based on wet weight of food; greens included Panicum hemitomum, P. virgatum, and Spartina patens.
- 4 Estimated using equation 3-17 (Calder and Braun, 1983) and body weights from Sather (1958).
- 5 Estimated using equation 3-20 (Stahl, 1967) and body weights from Sather (1958).
- 6 Estimated using equation 3-22 (Stahl, 1967) and body weights from Sather (1958).
- 7 Cited in Perry (1982.)

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2.2.11. Eastern Cottontail (rabbits)

Order Lagomorpha Family Leporidae. Rabbits and hares are medium-sized grazing herbivores found throughout North America. Most species are nocturnal and crepuscular. Many are social, travelling in small groups. Rabbits are prey for large carnivorous birds and mammals. Most species also are important game animals.

Selected species

The eastern cottontail (*Sylvilagus floridanus*) is the most widely distributed of the medium-sized rabbits (Chapman et al., 1982). It is found over most of the eastern half of the United States and southern Canada and has been widely introduced into the western United States (Chapman et al., 1980). North of Mexico, 14 subspecies are recognized (Chapman et al., 1982). The eastern cottontail feeds on green vegetation in summer and bark and twigs in winter. The cottontail is active from early evening to late morning and is preyed on by owls, hawks, and carnivorous mammals (Palmer and Fowler, 1975; Burt and Grossenheider, 1980).

Body size. The eastern cottontail measures 35 to 43 cm in length and weighs 0.7 to 1.8 kg (Lord, 1963; see table) with females slightly larger than the males (Nowak and Paradiso, 1983; see table). Cottontail body weight varies seasonally, increasing during spring and summer and declining during winter in some areas; different patterns occur in other areas (Chapman et al., 1982; Pelton and Jenkins, 1970).

Habitat. The eastern cottontail is unique to the genus because of the large variety of habitats that it occupies, including glades and woodlands, deserts, swamps, prairies, hardwood forests, rain forests, and boreal forests (Nowak and Paradiso, 1983). Open grassy areas generally are used for foraging at night, whereas dense, heavy cover typically is used for shelter during the day (Chapman et al., 1982). During winter, cottontails rely more on woody vegetation for adequate cover (Allen, 1984).

Food habits. During the growing season, cottontails eat herbaceous plants (e.g., grasses, clover, timoth, alfalfa). During the winter in areas where herbaceous plants are not available, they consume woody vines, shrubs, and trees (e.g., birch, maple, apple) (Chapman et al., 1982). In Ohio, bluegrass and other grasses made up a large portion of the eastern cottontail's diet, except during snow cover (Chapman et al., 1982). During the winter in Connecticut, the principle diet of eastern and New England cottontails consists of bark and twigs, shrubs and vines, berries, and willow (Dalke and Sime, 1941). In agricultural areas, corn, soybeans, wheat, and other crops may comprise a large portion of their diet (Chapman et al., 1982). Younger rabbits prefer the more succulent weedy forbs that contain more digestible energy and protein (Chapman et al., 1982). Coprophagy (ingestion of feces) has been reported in *S. floridanus* (Kirkpatrick, 1956).

Temperature regulation and molt. Eastern cottontails do not undergo hibernation or torpor; they are active all year, showing peaks of daily activity at dawn and dusk (Chapman et al., 1980). Adults molt gradually over about 9 mo of the year, with two peak molting periods (Spinner, 1940). In Connecticut, the spring peak occurs in May and

June and the fall peak occurs in September and October (Spinner, 1940). In Texas, spring and fall molts peak in April and October, respectively (Bothma and Teer, 1982).

Breeding activities and social organization. Breeding activity begins later at higher elevations and at higher latitudes (Conaway et al., 1974), by January in Alabama and by late March in southern Wisconsin (Chapman et al., 1980). Several studies have shown that continued harsh winter weather may delay the onset of the breeding season (Hamilton, 1940; Conaway and Wight, 1962; Wight and Conaway, 1961). Breeding seasons are longer in the southern states (Lord, 1960). The onset of breeding varies between different populations and within the same population from year to year (Chapman et al., 1980). Males may fight to establish dominance hierarchies for access to females (Chapman and Ceballos, 1990; Nowak and Paradiso, 1983). Lagomorphs in general are induced ovulators, and cottontails in particular demonstrate a synchronized breeding season, with conception immediately after the birth of a litter (Chapman et al., 1982).

Home range and resources. Cottontails are found in a variety of habitats that contain weedy forbs and perennial grasses; they prefer thick, short, woody perennials that provide escape sites (Chapman and Ceballos, 1990). Cottontails usually do not defend territories; the home ranges of different age and sex groups tend to overlap, especially in fall and winter when they look for areas offering a combination of food and cover (Chapman et al., 1980, 1982). Home ranges are smaller when thick vegetation provides abundant food and larger in habitats with less food (Chapman et al., 1982). Home ranges also are smaller during severe winter weather than at other times (Chapman et al., 1982). During the breeding season, females build elaborate nests within slanting holes in the ground where they give birth to their altricial (helpless) young. These burrows are vulnerable to flooding (Chapman et al., 1982). The size of male home ranges during the breeding season can be more than double that in winter (Nowak and Paradiso, 1983; Trent and Rongstad, 1974).

Population density. Population density depends on the availability of resources (e.g., food, cover) in an area, and tends to cycle over a period of several years (Chapman and Ceballos, 1990). Usual densities range from 1 to 5 animals per hectare, although values as high as 14 per hectare have been reported (Chapman and Ceballos, 1990; Chapman et al., 1982).

Population dynamics. The eastern cottontail exhibits the highest fecundity of the genus; they often produce 25 to 35 young per year (Chapman and Ceballos, 1990). Gestation lasts approximately 1 mo (Chapman et al., 1982). Females may produce five to seven litters per year, and juvenile breeding has been reported (Chapman et al., 1982). The first and last litters of the year are usually the smallest (Chapman et al., 1977). Cottontails have more litters with fewer young each in the southern states (Lord, 1960). Young leave the nest when about age 14 to 16 d, although they may not be fully weaned until a few weeks later (Ecke, 1955). Female cottontails are capable of breeding by age 5 mo, and males as early as 3 mo (Bothma and Teer, 1977). Adult mortality is high, from approximately 65 to 75 percent per year in some places (Eberhardt et al., 1963). Juvenile mortality is even higher, between 85 and 90 percent in the same areas (Eberhardt et al., 1963).

Similar species (from general references)

- The mountain cottontail (*Sylvilagus nuttallii*) (Nuttall's cottontail) is smaller (30 to 36 cm in length and 0.7 to 1.3 kg) than the eastern cottontail. The only cottontail through most of its range the western United States it lives in thickets and sagebrush, around loose rocks, cliffs, and mountains. In the southwest, it lives in forests.
- The New England cottontail (*Sylvilagus transitionalis*) is similar in size to the eastern cottontail and inhabits brushy areas, open forests, and mountain terrain in New England, extending down the Appalachians into the southern United States. In recent years, it has disappeared throughout much of the northeastern United States, apparently because of competition with *S. floridanus*.
- The desert cottontail (*Sylvilagus audubonii*) (Audubon's cottontail) (30 to 38 cm in length and 0.6 to 1.2 kg) is common in valleys in the arid southwest, although its range extends south to Mexico and north into the Rocky Mountains. It inhabits open plains, foothills, and low valleys and also areas of grass, sagebrush, pinyons and junipers. It is most active from late afternoon throughout the night.
- The brush rabbit (*Sylvilagus bachmani*) (28 to 33 cm; 0.6 to 0.8 kg) is usually seen around thick cover and rarely uses a burrow. It feeds on green vegetation, including lawns when in suburban areas. The species is found along the Pacific coast from the Columbia River in the north to the tip of Baja California in the south.
- The marsh rabbit (*Sylvilagus palustris*) is similar in size to the eastern cottontail and ranges from southeastern North Carolina to Florida. As the name implies, it inhabits swamps and hummocks, as well as wet bottomlands. Mostly nocturnal, it feeds on marsh vegetation, rhizomes, and bulbs.
- The swamp rabbit (*Sylvilagus aquaticus*) is similar in size to the eastern cottontail and is a good swimmer found in swamps, marshes, and wet bottomlands. It ranges primarily in the south, from Texas eastward. It nests beneath logs or in the bases of stumps, rarely using a burrow and may harm crops near swamps.
- The pygmy rabbit (*Sylvilagus idahoensis*) is markedly smaller (22 to 28 cm; 0.2 to 0.5 kg) than the eastern cottontail, lacks a conspicuous tail, and is considered by some to be a distinct genus (*Brachylagus*). Its range is limited to several western states, where it inhabits clumps of tall sagebrush. It is mostly nocturnal.
- The white-tailed jackrabbit (*Lepus townsendii*), larger (46 to 56 cm; 2.2 to 4.5 kg) than the eastern cottontail, is limited to the northern United States

west of the Great Lakes, into southern Canada. It inhabits open, grassy, or sagebrush plains and may damage hay crops and small trees.

- The black-tailed jackrabbit (*Lepus californicus*) (43 to 53 cm; 1.3 to 3.1 kg) is the most common jackrabbit in the grasslands and open areas of the western United States, where it inhabits open prairies and deserts with little vegetation. It is mostly nocturnal.
- The snowshoe hare (*Lepus americanus*) (33 to 46 cm; 0.9 to 1.8 kg) inhabits swamps, forests, and thickets in the northern United States and Canada. During summer, it feeds on succulent vegetation and during winter on twigs, buds, and bark. Its home range is about 4 ha, but populations fluctuate widely.

General references

Allen (1984); Burt and Grossenheider (1980); Chapman et al. (1980, 1982); Lord (1963); Nowak and Paradiso (1983); and Palmer and Fowler (1975).

Factors	Age/Sex/ Cond./Seas.	Mean	Range or (95% CI of mean)	Location (subspecies)	Reference	Note No.
	A M A F	1,134 ± 122 SD 1,244 ± 165 SD	801 - 1,411 842 - 1,533	w Maryland, West Virginia	Chapman & Morgan, 1973	
	A B winter A B spring A B summer A B fall A B not breed.	1,176 1,286 1,197 1,255 1,229 ± 113 SD	793 - 1,671 898 - 1,630 910 - 1,608 886 - 1,669	Georgia all areas combined Georgia mountain	Pelton & Jenkins, 1970 Pelton & Jenkins, 1970	
	A B not breed. A B not breed. A B not breed.	1,313 ± 141 SD 1,132 ± 136 SD	986 - 1,671 793 - 1,579	coastal Piedmont	renon a Jenkins, 1970	
A B neonate age: 10 d 30 d 50 d 101 d 149 d	AB	1,231 ± 164	700 - 1,800	Illinois	Lord, 1963	
	neonate	42.2	36.0 - 49.0	Alabama	Hill, 1972b	
	58 159 401 822 1,106		Illinois	Lord, 1963		
Growth Rate (g/d)	day 0 - 30 day 11 - 30 day 31 - 50 day 51 - 100 day 101 - 150	3.2 3.7 8.8 11.3 6.4		Illinois	Lord, 1963	
Metabolic Rate (kcal/kg-d)	A B basal	71			estimated	1
(A B free-living	203	(77 - 535)		estimated	2
Food Ingestion Rate (g/g-d)						3
Water Ingestion Rate (g/g-d)	АВ	0.097			estimated	4

Factors	Age/Sex/ Cond./Seas.	Mean	(60		Location (subspecies)	Reference	Note No.
Inhalation Rate (m³/d)	AB	0.63				estimated	5
Surface Area (cm²)	АВ	1,254				estimated	6
Dietary Composition	Spring	Summer	Fall	Winter	Location (subspecies)/ Habitat(measure)	Reference	Note No.
Composition	Spring	Summer	Fall	vviiitei	Habitat(illeasure)	Reference	NO.
trees	13	2	7	39	Connecticut (mallarus)/	Dalke & Sime, 1941	
shrubs & vines	4	2	27	40	various	(85% for mallarus	
herbs	44	23	34	5		subspecies,	
grasses, sedges,	,				(% frequence of occurrence;	remainder for similar	
rushes	26	56	30	6	observations of feeding on	species S. transitionalis)	
crops	13	17	2	10	plants)		
woody plants	17	23	20	100	Maryland/forest	Spencer & Chapman, 1986	
forbs	19	30	46				
grasses	64	47	34		(% frequency of occurrence;		
					stomach contents)		
bluegrass	34	34	25	32	Ohio (<i>mearnsi</i>)/NS	Dusi, 1952	
orchard grass	4	1		1	, and the same of		
timothy grass	5	12	7	1 i	(% frequency of occurrence;		
Nodding wild rye		11	8	4	scats)		
Canada goldenro		_	3	_	,		
red clover	_	_	6	_	(in winter, woody tissues		
unidentified	52	42	51	62	predominated in the		
					unidentified category)		

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location (subspecies)/Habitat	Reference	Note No.
Home Range Size (ha)	A M winter A F winter	3.05 ± 0.72 SE 2.99 ± 0.28 SE		Wisconsin/woodlot	Dixon et al., 1981	
	A M winter A M spring A M summer A M fall	3.2 7.2 7.8 3.1		c Pennsylvania/mixed	Althoff and Storm, 1989	
	A F winter A F spring A F summer A F fall	2.1 2.8 2.4 1.5		c Pennsylvania/mixed	Althoff and Storm, 1989	
	A M spring A M early summer late summer A F spring A F summer	2.8 4.0 1.5 1.7 0.8		sw Wisconsin/woodlot	Trent & Rongstad, 1974	
Population Density (N/ha)	fall	1.1 ± 0.41 SD	0.41 to 2.08 3.0 - 5.9	c Michigan/woods, marsh, fields Illinois/old field	Eberhardt et al., 1963 Lord & Casteel, 1960	
	winter summer fall spring	4.2 10.1 3.7	0.67 - 1.5	sw Wisconsin/farm	Trent & Rongstad, 1974	
Litter Size		3.5 ± 0.042 SE 5.3 6.0		Alabama/across six habitats Illinois/NS Missouri/wildlife area	Hill, 1972c Lord, 1963 Conaway et al., 1963	
Litters/Year		4.6	5 - 7	w Maryland/NS several locations and habitats	Chapman et al., 1977 Chapman et al., 1980	7
Days Gestation		28	25 - 35	several locations and habitats	Chapman et al., 1982	

Population Dynamics	Age/Sex/ Cond./Seas.	Mean	Range	Location (subspecies)/Habitat	Reference	Note No.
Age at Weaning		20 - 25 days		Illinois/NS	Ecke, 1955	
Age at Sexual Maturity	F M		3 - 6 months 3 - 6 months	s Texas/grassland Missouri/NS	Lord, 1961, Negus, 1959b Conaway & Wight, 1963	8
Annual Mortality	ВВ	80		sw Wisconsin/farm	Trent & Rongstad, 1974	
Rates (%)	ВВ	65 ± 7 SD		Illinois/sanctuary	Lord, 1963	
Longevity	В	1.25		Kentucky/NS	Bruna, 1952	9
Seasonal Activity	Begin	Peak	End	Location	Reference	Note No.
Mating	mid-March year-round	January - April	mid-September	Connecticut s Texas	Dalke, 1942 Bothma & Teer, 1977	9
Parturition	April	May - July	August	wc New York	Hamilton, 1940	
Molt fall	August September	October Sept Oct.	December November	s Texas Connecticut	Bothma & Teer, 1982 Spinner, 1940	
spring	February March	April May - June	July August	s Texas Connecticut	Bothma & Teer, 1982 Spinner, 1940	

- 1 Estimated using equation 3-43 (Boddington, 1978) and body weights from Lord (1963).
- 2 Estimated using equation 3-46 (Nagy, 1987) and body weights from Lord (1963).
- 3 See Chapters 3 and 4 for approaches to estimating food ingestion rates.
- 4 Estimated using equation 3-17 (Calder and Braun, 1983) and body weights from Lord (1963).
- 5 Estimated using equation 3-20 (Stahl, 1967) and body weights from Lord (1963).
- 6 Estimated using equation 3-22 (Stahl, 1967) and body weights from Lord (1963).
- 7 Summary of several studies.
- 8 Cited in Conaway and Wight (1963).
- 9 Cited in Chapman et al. (1980).
- 10 Cited in Chapman et al. (1982).

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